RESILIENCE OF SHEEP TO LIMITED WATER AVAILABILITY

By

ALI HUSSEIN HUSSEIN

Bachelor of Science in Animal Science
University of Minnesota
St. Paul, Minnesota
2013

Master of Science in Animal Science
Kansas State University
Manhattan, Kansas
2015

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Dissertation Approved:

Dr. Blake K. Wilson

Dissertation Adviser

Dr. Arthur L. Goetsch

Dr. Udaya E. DeSilva

Dr. Lionel J. Dawson

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Abstract: In 2 experiments, the objective was to establish performance, physiological, and nutritional assessments of hair sheep resilience to drinking water shortage. A total of 130 Dorper, Katahdin, and St. Croix female sheep with initial body weight of 60, 63, and 45 kg, respectively, were used. They were derived from the Midwest, Northwest, Southeast, and central Texas with all breeds representing the 4 climatic regions. In 4 separate 9-wk trials using different sheep over 2 yr, animals were housed individually, were fed a pelleted diet at 160% of the metabolizable energy requirement for maintenance, and were offered water ad libitum for 2 wk, 75% of ad libitum intake for 2 wk, and 50% of ad libitum intake for 5 wk in 3 consecutive periods. All animals were weighed 3 times and blood samples were collected 2 times each week. Data from the 4 trials were pooled and analyzed for effects of and interactions involving breed, region, period, week within period, and time of blood sampling within a week using different statistical models for different response variables. Across breeds and regions, the sheep decreased dry matter intake with advancing water restriction, gained weight when switched to 75% water restriction, suffered minor weight losses in wk 1 of 50% restriction, and gained weight in the remaining 4 wk of that restriction. Assessment of blood measurements and metabolites sensitive to water shortage revealed that across breeds and regions, all sheep exhibited minor changes in packed cell volume, hemoglobin concentration, plasma osmolality, and serum concentrations of albumin, cholesterol, creatinine, glucose, lactate, total protein, triglycerides, and urea under 75% water restriction. All sheep needed 1 wk to adapt to the severe water shortage of 50% and maintained levels of blood measurements and metabolites that were slightly higher than baseline values thereafter. In Experiment 2, nutrient digestibility and energy utilization of the diet fed in Experiment 1 were determined in a crossover design in which 11 St. Croix ewes were offered water at 50 or 100% of ad libitum intake. Water restriction increased apparent digestibility of dry matter, organic matter, neutral determent fiber, and crude protein, but did not affect energy utilization. It was concluded that the 3 hair sheep breeds had high resilience to limited water availability in the absence of heat stress and that improved digestibility of dietary nutrients was an adaptation mechanism that enabled them to gain weight under severe water shortage.

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LIST OF ABBREVIATIONS

Abbreviation	Definition
ADF	acid detergent fiber
ADG	average daily gain
ADH	antidiuretic hormone
AOAC	Association of Official Agricultural Chemists
B	breed
BG	black globe
BW	body weight
$BW^{0.75}$	metabolic body weight
^{o}C	degree Celsius
CH_4	methane
cm	centimeter
Co	cobalt
CO_2	carbon dioxide
CONT	control
CORR	correlation
CP	crude protein
Cu	copper
d	day

DE	digestible energy
dL	deciliter
DM	dry matter
DMI	dry matter intake
DOR	Dorper
e	base of the natural logarithm
e.g.	for example
Fe	iron
Fig.	Figure
g	gram
g	gravitational force
GE	gross energy
GI	gastrointestinal
GIS	Geographic Information System
GLM	general linear model
h	hour
Hb	hemoglobin
HE	heat energy
HLI	heat load index
HR	heart rate
I	iodine
i.e.	that is
IL	Illinois
Inc.	incorporation
IU	international unit

KAT	Katahdin
kg	kilogram
kJ	kilojoule
L	liter
LSD	least significant difference
LSMEANS	least squares means
m	meter
ME	metabolizable energy
mg	milligram
MJ	megajoule
mL	milliliter
mmol	millimole
Mn	manganese
mosm	milliosmole
MW	Midwest
N	nitrogen
n	number
NDF	neutral detergent fiber
NEON	National Ecological Observatory Network
ng	nanogram
NRC	National Research Council
NW	Northwest
O_2	oxygen
OM	organic matter
P	period

P	probability value
PCV	packed cell volume
PDIFF	piecewise differentiable
pg	picogram
pH	hydrogen ion concentration
R	region
RE	retained energy
REG	regression
REST	restricted
RH	relative humidity
s	second
SAS	Statistical Analysis System
SE	Southeast
SEM	standard error of the mean
sr	Spearman’s rank correlation coefficients
STC	St. Croix
T	time of blood sampling
THI	temperature-humidity index
TX	Texas
USDA	United States Department of Agriculture
vol	volume
vs.	versus
W	week within period
wk	week
WI	water intake

WS	wind speed
yr	year
Zn	zinc

CHAPTER I

INTRODUCTION

Limited drinking water availability for livestock, especially small ruminants such as sheep and goats, has been a growing problem in certain parts of the world as droughts become widespread and more severe due to climate change. Fortunately, small ruminants have several physiological adaptations that can help overcome the stresses caused by dehydration. These adaptations include mobilizing body reserves for nutrients and decreasing body water losses in the urine and feces and through evaporation. Urine water losses can be reduced by increasing water reabsorption in the kidneys, whereas fecal water losses can be decreased by promoting water absorption from the gut through osmosis due to elevated blood osmolality during dehydration. Water losses through evaporation via respiration and sweating, however, increase under heat stress.

As animals become more dehydrated, certain blood measurements and metabolites sensitive to drinking water shortage increase due to decreased plasma volume as a consequence to water losses. Elevated blood variables, including measurements such as packed cell volume, hemoglobin concentration, and plasma osmolality, are considered indicators of dehydration along with increased concentrations of albumin, cholesterol, creatinine, glucose, total protein, triglycerides, and urea in serum or plasma. Reduced performance variables such as feed intake and body weight are also considered useful indicators of dehydration because feed intake is commonly decreased with severe drinking water shortage and body weight losses usually result from mobilization of body reserves due to decreased feed intake and also from the animal's inability to replenish water losses. Resilience of small ruminants to water restriction, however, varies among species, breeds within a species, and individual animal within a breed. One strategy to improve such a resilience is to identify and use the most adapted animals in breeding or selection programs. Over several generations, this approach can potentially produce animals that are most efficient at water conservation during times of drinking water shortage. Although the physiological mechanisms of adaptation to limited drinking water availability are reasonably understood, many research challenges continue to hinder any potential efforts to improve resilience of sheep and goats to drought.

The goal of the research presented in this dissertation was to evaluate resilience of 3 hair sheep breeds (i.e., Dorper, Katahdin, and St. Croix) that have been increasingly spreading worldwide, including in the U.S. Chapter 2 of the dissertation explains the known physiological responses to water restriction and reviews published reports on limited water availability in sheep and goats. It also explains how performance and blood variables were affected across the limited number of published studies, which varied in water-restriction strategies, types of the tested animals, and experimental conditions. Chapter 3 evaluates the performance responses of 130 females of the 3 hair sheep breeds, which represented 4 climatic regions in the U.S., to water restriction under controlled conditions in 4 separate trials over 2 yr. In each trial, all sheep were offered water ad libitum for 2 wk, 75% of ad libitum intake for 2 wk, and 50% of ad libitum intake for 5 wk. Chapter 4 evaluates the physiological responses of the sheep in those 4 trials. Although presented in 2 separate manuscripts, Chapters 3 and 4 represent 2 parts of the same experiment. Chapter 5, however, evaluates responses in nutrient digestibility and energy utilization of St. Croix sheep to water restriction at 50% of ad libitum intake. Finally, Chapter 6 summarizes the implications of the research results presented in the dissertation.

CHAPTER II

REVIEW OF LITERATURE

INTRODUCTION

Water is the most important nutrient required to support life and animals use it for several functions such as dissolving nutrients, transport of molecules through blood, intracellular transport, milk production, urinary excretion, and regulation of body temperature by evaporative cooling (NRC, 2007). Unfortunately, limited availability of drinking water for livestock, including small ruminants, has been a growing problem in certain parts of the world as droughts become widespread and more severe due to climate change (Nardone et al., 2010; Sejian, 2013; Misra, 2014). As a result, expansion of droughts has made it difficult for livestock, in general, and small ruminants, in particular, to meet their water requirements for optimal health and production (Nardone et al., 2010). Fortunately, small ruminants have several physiological adaptation mechanisms that can help overcome stresses associated with water scarcity (Parrot et al., 1996; Silanikove, 2000a; Chedid et al, 2014). Those mechanism include mobilizing body reserves for nutrients and decreasing body water losses in urine and feces and via evaporation.

Notably, the ability of animals to rapidly adapt to and recover from environmental stressors such as limited water availability demonstrates resilience that varies between sheep and goats, among breeds of each species, and among individuals within a specific breed. Nevertheless, any efforts to improve resilience of small ruminants to a stressor such as drinking water shortage would depend on understanding of the physiological mechanisms many animals use to cope with limited water availability and of how they differ in their adaptation. Parameters that have been used to evaluate those adaptation mechanisms include feed dry matter intake (DMI), body weight (BW), and blood measurements (e.g., packed cell volume [PCV], hemoglobin [Hb] concentration, and osmolality), metabolites (e.g., albumin, cholesterol, creatinine, glucose, total protein, triglycerides, and urea) and hormones (e.g., aldosterone, cortisol, and vasopressin) sensitive to water shortage (Chedid et al., 2014). Such an understanding would help in selection of animals efficient at water conservation and able to produce at levels matching their genetic potential under environmental stressors such as drought. The objective of this review is to evaluate the effects of water restriction on small ruminants, especially sheep and goats, and to assess their potential adaptations to drought conditions.

RESTRICTION OF WATER INTAKE BY RUMINANTS

The primary cause of restricting water intake (WI) by ruminants is its limited availability due to prolonged periods of drought (Nardone et al., 2010). For this reason, water shortage is most common in arid and semiarid environments such as Australia, central Africa, southwest Asia, and southwest of the U.S., including Arizona, New Mexico, and Nevada (Misra, 2014). However, climate change has recently caused droughts in other areas of the world where it was previously uncommon, including

Southeast Asia (e.g., Cambodia), South America (e.g., Brazil and Bolivia), West Africa (e.g., Mauritania), Central America (e.g., Honduras and Nicaragua), and parts of the U.S. such as California and Oklahoma (Misra, 2014). By receiving less than normal rainfall in these areas, rivers, lakes, and other water reservoirs start to dry up.

The lack of clean drinking water can also result in water restriction as ruminants either refuse to drink or decrease their intake of contaminated or polluted water that negatively affects health and production. Examples include water with high levels of total dissolved solids (Kattnig et al., 1992; Alves et al., 2017; Sharma et al., 2017), sulfate (Beke and Hironaka, 1991; Loneragan et al., 2001; Grout et al., 2006), and nitrate (Seerley et al., 1965). Water restriction can also result from management practices such as overcrowding which creates resource competition among animals where aggressive ones consume adequate water and submissive ones consume less (Ehrlenbruch et al., 2010). This type of competition most often occurs when water is found in only one location and, as a result, all animals are forced to go there to drink (Ehrlenbruch et al., 2010). Similarly, not offering water frequently enough is another mismanagement that could result in water restriction. If limited amounts of water are offered only once per day, thirst sensation may increase and encourage the animals to drink all water within the first few minutes of provision, a drinking behavior that would make water unavailable for consumption until the next day (Kraly, 1984). Offering water once per day could also exacerbate competition within pens because aggressive animals that are thirsty may consume greater quantities of water than when satisfactory amounts are offered throughout the day (Coimbra et al., 2012). In this case, submissive animals would consume less water or none at all (Ehrlenbruch et al., 2010).

Although not considered water restriction per se, dehydration can also be induced by heat stress conditions. When animals are exposed to heat stress, a compensatory mechanism for maintaining body temperature increases evaporation of water from the body, which causes a cooling effect because water has a high rate of vaporization (NRC, 2007). As more body water is evaporated to dissipate heat loads from the environment, however, less water is retained, which prompts the need for increased WI to replenish the water lost to keep the animal thermoneutral. In most arid regions, however, animals are unable to consume enough water to restore evaporative losses because reduced water availability and increased heat stress often occur together (Chedid et al., 2014). In those regions, animals will use various mechanisms to decrease water losses through evaporation as well as other losses of body water (Monty et al., 1991; Marai et al., 2007; Chedid et al., 2014).

BODY WATER LOSSES

Evaporative Water

Evaporation of water represents approximately 25% of whole body water losses during thermoneutral conditions and can increase to 70% of water losses during heat stress (NRC, 2007). The modes of water losses through evaporation include respiration through the lungs, sensible losses through skin (convection and conduction), and sweating. In species that have poorly developed sweat glands, such as sheep and goats, water loss from sweating is minor (0 to 5%) relative to respiration and sensible skin losses (NRC, 2007), which explains why sheep and goats undergoing heat stress are most often seen panting. However, high humidity conditions can inhibit the animal’s ability to dissipate heat through evaporation if the water vapor gradient is higher outside than inside the body. To overcome this challenge, sheep (Monty et al., 1991; Dixon et al., 1999; Alhidary et al., 2012) and goats (Lu, 1989; Hamzaoui et al., 2013; Salama et al., 2014) minimize internal heat production by decreasing DMI, which subsequently results in less internal heat production from metabolism (Marai et al., 2007). However, both species seem to differ in their ability to handle heat stress when subjected to drinking water shortage. Under low humidity (e.g., 10 to 15%), for example, sheep exhibited 5-fold greater panting than goats when their WI was restricted to 50% of ad libitum under heat stress (39 ^{o}C) with the difference being attributed to the sheep's lesser ability to dissipate heat through the skin (Rahardja et al., 2011). Unlike goats, many sheep breeds have a thick wool coat that insulates heat and hinders its ability to leave the body through the skin with the type (McArthur, 1980) and color (Cena and Monteith, 1975) of wool influencing the degree of heat dissipation (Silanikove, 2000b).

Urinary Water

On average, urine constitutes 60% of daily water losses (NRC, 2007), a percentage subject to change depending on dietary and environmental factors. As to the former, an increase in dietary protein intake, for example, generally results in greater urine output because excess nitrogen (N) from protein is converted to urea in the liver and excreted in the urine (Cocimano and Leng, 1967). Notably, urea molecules partitioned to the kidney for excretion generate an osmotic pull of water into the urinary tract as water moves from areas of low concentration to those of high concentration to dilute urea in the urine (Weiner et al., 2015). However, small ruminants have the ability to concentrate urine and decrease urinary water excretion under harsh conditions, especially high environmental temperatures and droughts (Parrot et al., 1996; Silanikove, 2000a; Chedid et al., 2014). An extreme example of this adaptation was demonstrated in Awassi sheep, a fat-tailed Middle Eastern breed known for resilience to water shortage, as they decreased urine volume from 1,278 to 120 mL/d and increased both its osmolality and urea concentration from 1,352 to 1,924 mosm/L and from 340 to 5,425 mg/dL, respectively, after being deprived of water for 5 d (Laden et al., 1987).

In general, decreasing urinary water loss is considered one of the primary means of conserving body water when WI is less than optimal and is accomplished by two separate mechanisms. The first involves osmoreceptors that detects increases in solute concentrations (osmolality) in the bloodstream during dehydration and sends a neural signal to the hypothalamus to trigger secretion of vasopressin (antidiuretic hormone; ADH) from the posterior pituitary gland (Dibas et al., 1998). Vasopressin then travels to the kidneys, binds to receptors in the distal or collecting tubules, and promotes reabsorbtion of water back into the circulation through an intracellular signal transduction cascade triggering insertion of aquaporin-2 transporters into the apical membrane of cells (Dibas et al., 1998). The second mechanism is mediated by the renin-angiotensin-aldosterone system, which is a multistep pathway responsible for maintaining blood pressure (Friis et al., 2013). This pathway begins when baroreceptors detect a decrease in blood pressure and, in response, neurons send a neural signal (acetylcholine) to the Juxtaglomerular cells in the kidney to produce the hormone renin, which converts angiotensinogen to angiotensin I. Next, angiotensin-converting enzyme converts angiotensin I to angiotensin II, which stimulates synthesis and secretion of aldosterone from the adrenal gland. Aldosterone then initiates several reactions that increase reabsorption of sodium from the kidney's distal tubules of nephrons which triggers reabsorption of water through osmosis (Atlas, 2007).

Fecal Water

Fecal water losses constitute approximately 15 to 25% of water losses from the body (NRC, 2007). In contrast to monogastric animals and cattle, small ruminants excrete the least amount of water in their feces, which explains why sheep and goats have pelleted fecal material. Their feces get even drier during water restriction as more water is absorbed from the gastrointestinal (GI) tract into the blood through vasopressin's actions (Olsson, 2005). Awassi sheep, for example, excreted almost dry feces (11.9 vs. 52.6% water) after being deprived of water for 5 d (Laden et al., 1987). Notably, the water movement from the lumen of the GI tract into blood is driven by osmotic gradient generated by dehydration due to decreased blood volume and increased blood osmolality (Chedid et al., 2014). This osmotic gradient increases efficiency of water reabsorption and helps maintain isotonic conditions between blood and the lumen of the GI tract (Kiil, 1989). Efficiency of water reabsorption is also improved by decreased liquid passage through the GI tract as the rumen acts as a water reservoir, especially under conditions of drinking water shortage (Silanikove, 1994).

PERFORMANCE RESPONSES TO WATER RESTRICTION

Measurements such as DMI and BW have been routinely used as indicators to assess ability of small ruminants to cope with limited drinking water availability. Though many studies consistently demonstrated decreases in DMI and BW during water restriction, the magnitude of the reported responses usually reflected the severity of the dehydration tested.

Feed Intake

In the absence of heat stress, DMI is positively correlated with WI (Kraly, 1984; Laden et al., 1987; Silanikove, 1992). However, inconsistent responses of sheep and goats to water restriction have been reported. For example, Casamassima et al. (2008) did not detect differences in DMI by Comisana ewes offered water at 100, 80, or 60% of ad libitum intake for 6 wk. In contrast, offering Lacaune ewes water at 80 or 60% of ad libitum intake decreased DMI by 16 and 36%, respectively, at the end of a 4-wk trial (Casamassima et al., 2016). Offering Baluchi lambs water low or high in total dissolved solids at 50% of ad libitum intake for 6 wk decreased DMI by 40 and 42%, respectively (Vosooghi-Postindozet al., 2018). Using intermittent watering regimes, Jaber et al. (2004) also reported 24 and 44% decreases in DMI when non-lactating Awassi ewes were offered water every 2 or 4 d, respectively, as compared to control ewes offered water daily.

Research with goats showed in a 4-wk trial that DMI by crossbred German Fawn does was not altered by restricting WI to 87 or 73% of ad libitum, but decreased by 13% when water was restricted to 56% of ad libitum intake (Kaliber et al., 2016). In a 15-wk trial, restriction of WI by desert goats to about 40% of ad libitum tended to decrease DMI of good and poor quality hays by 19 and 21%, respectively (Ahmed and El Kheir, 2004), whereas restricting WI of Aardi does to 75 and 50% of ad libitum over 6 d in a hot environment (approaching 50 ºC) decreased DMI by 14 and 22%, respectively (Alamer, 2009). Using both species, Mengistu et al. (2016) reported that DMI decreased by 30.6 and 43.8% for Katahdin sheep, 22.4 and 34.4% for Boer goats, and 19.1 and 35.2% for

Spanish goats when their WI was restricted gradually by 10% from 100% to 50 and 40% of ad libitum, respectively.

The variable response in DMI by small ruminants to limited drinking water availability suggests that there is a threshold that needs to be reached before reduced WI affects feed intake. Nevertheless, DMI by water-restricted animals seems to be influenced by weather conditions, animal factors, and the diet. High environmental temperatures have been shown to exacerbate the adverse effects of water shortage (Alamer, 2009). Younger animals (Mengistu et al., 2016; Vosooghi-Postindozet al., 2018) also seem to be less able to cope with water shortage than mature animals (Casamassima et al., 2008, 2016). As to the diet, DMI was influenced by the quality of the forage fed to water-restricted goats (Ahmed and El Kheir, 2004; Morand-Fehr, 2005).

Body Weight

Under intermittent watering regimes, it has been shown that despite their resilience to drinking water shortage, Awassi ewes suffered BW losses as a consequence to water restrictions (Jaber et al., 2004; Hamadeh et al., 2006; Ghanem et al., 2008). Those losses were minor when dry ewes were offered water every 2 or 4 d for 6 wk (1.2 and 5.4%, respectively; Jaber et al., 2004) or every 4 d for 12 d (6.9%; Ghanem et al., 2008). Larger BW losses, however, occurred when dry and lactating ewes were offered water every 3 d for 3 wk (16.7 and 26.2%, respectively; Hamadeh et al., 2006). Variable BW losses were also reported when sheep or goats were offered water daily but in restricted amounts. Examples included decreases in average daily gain by 64 and 75% when Baluchi lambs were offered water low or high in total dissolved solids, respectively, at 50% of ad libitum intake for 6 wk (Vosooghi-Postindozet al., 2018) and losses in BW of 6 and 8% when Aardi does were offered water at 75 and 50% of ad libitum intake for 6 d, respectively (Alamer, 2009). A 7.1% loss in BW was also reported for crossbred German Fawn does when their WI was restricted to 56% of ad libitum (Kaliber et al., 2016). Using sheep and goats, Mengistu et al. (2016) reported BW losses of 12.7 and 13.2% across species when WI was restricted gradually by 10% from 100% to 40% of ad libitum over 7 or 14 wk, respectively. In all cases, the BW loss was attributed to loss of body water and/or mobilization of body fat to compensate for reduced DMI.

In other studies, however, no changes in BW, total body water, or DMI were reported when WI was restricted. Examples included offering water at 57 and 79% of ad libitum intake to Australian feral goats (Freudenberger and Hume, 1993) and Sirohi, Marwari, and Kutchi goats (Misra and Singh, 2002). The lack of BW change in these studies suggested that the water restriction treatments used were not severe enough considering that in both cases the goats were not under heat stress.

Improved Digestion

Some studies suggested that reductions in DMI by water-restricted sheep or goats were compensated for, in part, by increased digestibility of and improved nutrient utilization from the feed consumed (Asplund and Pfander, 1972; Hadjigeorgiou et al., 2000; Ahmed and Ammar, 2001). Evidence supporting this suggestion showed that offering water to desert (black Bedouin) and non-desert (Swiss Saanen) goats every 3 d decreased DMI by 11.9 and 39.7 g/kg $BW^{0.75}$, respectively, and increased DM digestibility of alfalfa hay from 71.6 to 74.1% and from 66.8 to 71.2%, respectively (Silanikove, 1985). Restricting WI by Baluchi lambs to 50% of ad libitum also increased digestibilies of organic matter (OM), neutral detergent fiber (NDF), acid detergent fiber (ADF), and crude protein (CP) of a diet containing 40% alfalfa hay by 1.4, 2.5, 1.9, and 2.3 percentage units, respectively (Vosooghi-Postindoz et al., 2018). In contrast, restricting water offered to Corriedale ewes from ad libitum to only 2 h daily did not affect DMI but increased digestibilities of OM, NDF, ADF, and CP of a maintenance diet by 4.0, 6.6, 6.0, and 3.9 percentage units, respectively, decreased urinary N from 9.86 to 8.23 g/d, and increased retained N from 20.0 to 31.1% of N intake (Nejad et al., 2014). In those cases, the improved digestibilities were attributed to slower rate of digesta passage and longer retention time of digesta in the GI tract due to decreased DMI (Van Soest, 1982) or slower rate of fluid passage due to water restriction (Kaske and Groth, 1997). Rate of digesta passage was shown to be directly influenced by the quantity of water consumed (Kaske and Groth, 1997) and passage rate of fluid through the GI tract was also shown to decrease as an adaptation mechanism by water-restricted sheep and goats in order to use the rumen as a water reservoir and retain more water in the body (Silanikove, 1994).

It is worth noting that no improvements in nutrient digestibility or utilization were reported in some water restriction studies. Freudenberger and Hume (1993) showed that digestibilities of DM and ADF were not altered when mature goats having free access to alfalfa hay were restricted to 57% of ad libitum WI. Hadjigeorgioua et al. (2000) also did not detect any change in disgestibilities of DM, NDF, ADF, or CP when Karagouniko sheep having free access to alfalfa hay were offered water ad libitum, at 65% of ad libitum intake, or for 1 h daily. Considering that the goats and sheep in those studies were fed chopped alfalfa hay of different CP contents (8.1 vs. 12.8%, respectively), it is possible that other factors have contributed to the lack of improvement in digestibility.

PHYSIOLOGICAL RESPONSES TO WATER RESTRICTION

When small ruminants become dehydrated during water restriction, plasma volume decreases due to water uptake by tissue cells, including red blood cells (Schaefer et al., 1990). A clear example was demonstrated in decreases of BW, total body water volume, extracellular fluid volume, and plasma volume by 16.3, 22.0, 35.1, and 41.7%, respectively, after Dorper sheep were deprived of water for 4 d (Degan and Kam, 1992). Hyperosmolality due to increased solute concentrations is, thus, commonly detected in water-restricted animals (Qinisa et al., 2011). Reduced plasma volume also increases concentrations of certain blood components and forces sheep (Chedid et al., 2014) and goats (Silanikove, 2000b) to activate physiological mechanisms to adapt to dehydration and cope with limited drinking water availability. Those mechanisms rely on hormonal responses that promote water reabsorption in the kidneys (Dibas et al., 1998; Atlas, 2007; Friis et al., 2013) and water absorption from the GI tract (Olsson, 2005) to gradually decrease solute concentrations and osmolality as blood vessels refill with water. In addition to those adaptation mechanisms to maintain plasma volume by decreasing water losses, small ruminants efficiently use the rumen as a water reservoir to replenish immediate losses in plasma volume through osmosis (Silanikove, 1994). Using a fluid marker for the rumen contents, Dahlborn and Holtenius (1990) demonstrated absorption of the labeled water through the rumen wall and its immediate impact on decreasing plasma osmolality in dehydrated sheep. It is important, therefore, to assess physiological responses of small ruminants to water restriction in order to understand how certain sheep or goats are more able to cope with the stress associated with drinking water shortage. Thus, certain blood measurements and metabolites sensitive to drinking water shortage and hormones involved in the physiological responses to dehydration have been evaluated in some water restriction studies. However, those studies varied in their approach, with the majority used infrequent watering regimes and some offered water daily in restricted amounts of ad libitum intake.

Inconsistent Responses among Studies

Variable physiological responses were reported when sheep or goats were offered water infrequently or deprived of water for a limited number of days. Offering water to Awassi ewes every 3 d for 23 d (Hamadeh et al., 2006) or every 4 d for 42 d (Jaber et al., 2004) did not affect PCV or concentrations of Hb and serum glucose, increased serum concentrations of cholesterol, creatinine, total protein, and urea, and showed contradictory effects on albumin concentration. Offering water to Awassi ewes every 4 d for 12 d, however, increased PCV, Hb concentration, and serum concentrations of albumin, cholesterol, and total protein, but did not affect glucose concentration (Ghanem et al., 2008). Water deprivation for 5 d also showed different results as it increased plasma osmolality and concentrations of creatinine and urea in Awassi ewes (Laden et al., 1987) and increased plasma concentrations of cholesterol, creatinine, and urea without affecting PCV or plasma concentrations of albumin and total protein in Yankasa ewes (Igbokwe, 1993). In contrast, depriving Hipsi, Aardi, and Zumri bucks of water for 3 d increased PCV in all breeds (Alamer, 2006), whereas offering Ethiopian Somali does water every 4 d for 32 d increased plasma osmolality and total protein concentration (Mengistu et al., 2007a). Plasma osmolality and total protein concentration similarly increased when Ethiopian Somali bucks were offered water every 4 d for 72 d (Mengistu et al., 2007b). Depriving Nubian does of water for 3 d also increased serum osmolality and total protein concentration as well as PCV and serum concentrations of albumin, creatinine and urea, but did not affect glucose concentration (Abdelatif et al., 2010).

Variable responses were also reported in studies where sheep or goats were offered water daily in restricted amounts. For example, restricting WI by Comisana ewes to 60% of ad libitum for 40 d increased serum concentrations of albumin, cholesterol, total protein, and triglycerides, but did not affect concentrations of creatinine, glucose, or urea (Casamassima et al., 2008). In another study by the same group, restricting WI by Lacaune ewes to 60% of ad libitum for 28 d increased PCV, Hb concentration, and serum concentrations of creatinine and total protein (Casamassima et al., 2016). Contradictory results were also reported when Malpura ewes were offered water at 60% of ad libitum intake for 28 d (De et al., 2015) or 35 d (Kumar et al., 2016). Whereas water restriction increased PCV and did not affect Hb concentration or plasma concentrations of albumin, cholesterol, glucose, and total protein (De et al., 2015), it decreased plasma concentrations of cholesterol and glucose without affecting PCV or concentrations of Hb or albumin (Kumar et al., 2016). Offering water low or high in total dissolved solids to Baluchi lambs at 50% of ad libitum for 42 d, however, increased PCV and concentrations of cholesterol and triglycerides without affecting Hb concentration or serum concentrations of albumin, creatinine, glucose, and total protein across the water salinity treatments (Vosooghi-Postindozet al., 2018). Restricting WI by Tswana and Boer goat wethers to 50% of ad libitum for 7 d increased PCV, plasma osmolality, and concentrations of total protein and urea across breeds (Qinisa et al., 2011), whereas restricting WI by crossbred German Fawn does to 87, 73, and 56% of ad libitum increased plasma concentrations of cholesterol, creatinine, glucose, and urea in a manner reflecting the severity of water shortage (Kaliber et al., 2016).

It is evident that water restriction in those studies did not consistently increase blood measurements or metabolite concentrations in response to the decrease in plasma volume that commonly occurs with water shortage. Thus, the variable responses could be attributed to differences in genetic potential among the various breeds of sheep or goats evaluated for their ability to cope with limited drinking water availability. They could also be attributed to other factors, including the presence or absence of heat stress, the nutritional and physiological states of the test animals, the severity of the water-restriction treatments, and the experimental designs of those studies. As a result, these factors must be considered in evaluating the impact of water restriction on small ruminants.

Changes in Blood Measurement

Elevated plasma osmolality (Laden et al., 1987; Mengistu et al., 2007a,b; Qinisa et al., 2011) and increased PCV (Alamer, 2006; Abdelatif et al., 2010; Vosooghi-Postindozet al., 2018), Hb concentration (Li et al., 2000), or both (Ghanem et al., 2008; Casamassima et al., 2016) in water restricted sheep or goats have been attributed to decreased plasma volume. Although, plasma volume was not measured in any of those studies, plasma osmolality, PCV, and Hb concentrations have been considered good indicators of dehydration in small ruminants (Laden et al., 1987; Dahlborn et al., 1988; Abdelatif and Ahmed, 1994). The impact of plasma volume on PCV as an example of those blood measurements was demonstrated in sheep and goats when WI was restricted to 50% of ad libitum under different ranges of environmental temperatures (18 to 30 ^{o}C and 18 to 39 ^{o}C; Rahardja et al., 2011). Across those temperatures, water restriction decreased plasma volume (57.7 vs. 59.6 mL/kg$^{0.82}$ and 52.2 vs. 55.9 mL/kg$^{0.82}$) and increased PCV (31.3 vs. 29.3% and 36.2 vs. 34.3%) in the sheep and goats, respectively. However, inconsistent results for plasma osmolality and concentrations of PCV and Hb have been reported in other water restriction studies. While osmolality was not affected (averaging 292 mosm/L) when sheep were deprived of water for 3 d under a controlled temperature of 24.8 ^{o}C (Li et al., 2000), large increases occurred with water deprivation of sheep for 5 d (328 vs. 278 mosm/L; Laden et al., 1987) and goats for 3 d (289 to 337 mosm/L; Alamer, 2006) in hot climates (up to 41 and 50 ^{o}C, respectively). In contrast, moderate increases in plasma osmolality occurred when goats were offered water every 4 d for 32 d (313 vs. 305 mosm/L; Mengistu et al., 2007a) or 72 d (314.0 vs. 304.0 mosm/L; Mengistu et al., 2007b) in a temperate climate (19 to 33 ^{o}C). In addition to the differences in coping with water shortage among dehydrated sheep or goats, plasma osmolality seemed to have been exacerbated by heat stress which reflects more body water losses and less plasma volume in hot environments.

Both PCV and Hb concentration also showed inconsistencies similar to those for plasma osmolality when small ruminants were subjected to drinking water shortage. Offering water to Awassi sheep every 3 d for 23 d (Hamadeh et al., 2006) or every 4 d for 42 d (Jaber et al., 2004) did not affect PCV (averaging 30.1 and 28.6%, respectively) or Hb concentrations (averaging 11.5 and 10.9 g/dL, respectively), whereas offering water to Awassi sheep under the same temperate climate every 4 d for 12 d (Ghanem et al., 2008) increased PCV (35.9 vs. 29.9%) and Hb concentration (15.5 vs. 13.6 g/dL). In other studies with sheep, water deprivation for 5 d did not affect PCV (averaging 27.3%; Igbokwe, 1993), but water deprivation for 3 d increased Hb concentration (12.6 vs. 11.4 g/dL) without affecting PCV (averaging 35.5%; Li et al., 2000). Restricting daily WI by sheep to 60% of ad libitum for 4 or 5 wk also did not affect PCV or Hb concentration (averaging 42.8% and 11.8 g/dL; Kumar et al., 2016), increased PCV (47.4 vs. 34.9%), but did not affect Hb concentration (averaging 13.9 g/dL; De et al., 2015), and increased both (30 vs. 24% and 11.9 vs. 10.1 g/dL, respectively; Casamassima et al., 2016). Increases in PCV were also reported when goats were deprived of water for 3 d (38.4 vs. 29.3%; Alamer, 2006) or when daily WI was restricted to 50% of ad libitum for 7 d (27.8 vs. 25.8%; Qinisa et al., 2011).

Changes in Blood Metabolites

Concentrations of metabolites such as albumin, cholesterol, creatinine, glucose, total protein, triglycerides, and urea in blood of small ruminants have been considered good indicators of dehydration and animals' ability to cope with water restriction. Those concentrations, which have been measured in serum or plasma, were used to reflect changes in plasma volume of dehydrated animals and/or changes in certain metabolites following reduced DMI under severe drinking water shortage.

Urea, a detoxifican product, is synthesized from ammonia in the liver, excreted by the kidneys to dispose of endogenous and excess dietary N, or recycled into the rumen through saliva and reabsorption across the rumen wall for utilization by the rumen bacteria (Huntington and Archibeque, 2000). Creatinine, another nitrogenous compound, is produced in the muscles and excreted by the kidneys in proportion to the muscle mass and the rate of proteolysis (Caldeira et al., 2007a). Under conditions of drinking water shortage, however, the kidney function is altered (Kataria and Kataria, 2007) with slower glomerular filtration and higher urea reabsorption (Marini et al., 2004), leading to increased blood concentrations of creatinine and urea. Offering water to Awassi ewes every 3 d (Hamadeh et al., 2006) or 4 d (Jaber et al., 2004), for example, increased serum concentrations of creatinine (1.09 vs. 0.9 and 1.14 vs. 0.96 mg/dL, respectively) and urea (60.1 vs. 49.8 and 46.3 vs. 35.8 mg/dL, respectively). Depriving Awassi (Laden et al., 1987) and Yankasa (Igbokwe, 1993) ewes of water for 5 d also increased serum concentrations of creatinine (1.5 vs. 0.8 and 1.54 vs. 1.05 mg/dL, respectively) and urea (111 vs. 44 and 121.9 vs. 44.4 mg/dL, respectively). Similar increases in concentrations of creatinine and urea (1.10 vs. 0.68 and 40.5 vs. 29.8 mg/dL, respectively) were reported when Nubian does were deprived of water for 3 d (Abdelatif et al., 2010). However, other studies with sheep showed that water restriction did not affect concentrations of creatinine (Li et al., 2000; Vosooghi-Postindozet al., 2018), urea (Nejad et al., 2014), or both (Casamassima et al., 2008).

In contrast to waste products such as creatinine and urea, blood concentrations of total protein and albumin reflect the protein status of the ruminant animal, with low concentrations indicating long-term deficiency in dietary protein (Caldeira et al., 2007a,b). Under low protein intake, albumin in blood acts as a labile protein reservoir of readily available amino acids until supply is made available through feeding or mobilization of skeletal muscles (Moorby et al., 2002). Albumin also plays an important role in osmoregulation, especially during dehydration (Burton, 1988). Considering these nutritional and physiological functions, Hamadeh et al. (2006) suggested that serum concentrations of total protein and albumin in water-restricted sheep are influenced, in part, by DMI. In their study, offering water to Awassi ewes every 3 d for 23 d increased serum concentrations of albumin (3.43 vs. 3.08 g/dL) and total protein (7.86 vs. 7.39 g/dL) despite intermediate changes. Concentrations of albumin and total protein peaked after the first 3 d of water deprivation, but their levels gradually decreased to approach those of the control ewes by the end of the trial as DMI also decreased. Concentrations of albumin and total protein increased (4.22 vs. 3.47 and 9.80 vs. 7.95 g/dL, respectively) in Awassi ewes offered water every 4 d (Ghanem et al., 2008) and also increased (4.3 vs. 3.0 and 8.9 vs. 7.1 g/dL, respectively) in Nubian does deprived of water for 3 d (Abdelatif et al., 2010). The elevated levels in both cases were attributed to reduced blood volume caused by water restriction (Degan and Kam, 1992). In contrast, concentrations of albumin and total protein did not change when Yankasa ewes were deprived of water for 5 d (Igbokwe, 1993) or when WI by Malpura ewes was restricted to 60% of ad libitum for 28 d (De et al., 2015).

Contradictory results were also found for blood glucose concentrations with no change in serum concentrations in sheep subjected to intermittent watering regimes (Jaber et al., 2004; Hamadeh et al., 2006; Ghanem et al., 2008) or offered water at 50% (Vosooghi-Postindozet al., 2018) and 60% (Casamassima et al., 2008; De et al., 2015) of ad libitum intake. In contrast, plasma glucose concentration decreased (46.3 vs. 51.2 mg/dL) and increased (70 vs. 57 mg/dL) when WI by Malpura ewes (Kumar et al., 2016) or crossbred German Fawn (Kaliber et al., 2016) was restricted to 60 and 56% of ad libitum, respectively. It is worth noting that because ingested glucose and starch are efficiently fermented to volatile fatty acids in the rumen, circulating glucose is derived from propionate and other non-carbohydrate precursors such as lactate, glycerol, and amino acids through gluconeogenesis (Baird et al., 1980), which is inhibited by reduced propionate production in the rumen in response to low DMI (Allen et al., 2009). Thus, it is expected that reductions in DMI due to dehydration would influence serum glucose concentrations.

Finally, blood concentrations of cholesterol and triglycerides have been shown to increase with drinking water shortage. Under intermittent watering regimes (Jaber et al., 2004; Hamadeh et al., 2006; Ghanem et al., 2008), serum cholesterol concentration consistently increased in water-restricted sheep (82.7 vs. 75.4, 92.8 vs. 65.7, and 79.6 vs. 62.2 mg/dL, respectively). Plasma cholesterol concentration also increased (62 vs. 47 mg/dL) when WI by goats was restricted to 56% of ad libitum (Kaliber et al., 2016). Serum concentrations of cholesterol (67.7 vs. 63.0 and 68.3 vs. 63.1 mg/dL) and triglycerides (19.5 vs. 16.8 and 32.5 vs. 30.9 mg/dL) also increased when WI by ewes (Casamassima et al., 2008) or lambs (Vosooghi-Postindozet al., 2018) was restricted to 60 or 50% of ad libitum, respectively. In those studies, the increased concentrations were attributed to decreased DMI and the subsequent need for fat mobilization to meet the shortfall in energy requirements. Contradictory responses, however, occurred as plasma cholesterol concentration either decreased (55.5 vs. 65.4 mg/dL; Kumar et al., 2016) or was not affected (De et al., 2015) when WI by non-pregnant Malpura ewes was restricted to 60% of ad libitum. Nevertheless, they could be attributed to the lack of severe reductions in DMI in both cases (56 vs. 59 and 52 vs. 55 g/kg $BW^{0.75}$, respectively) and, as a result, there was no shortage in energy supply or need for fat mobilization.

Hormonal Regulations

Vasopressin is considered the primary hormone responsible for reabsorption of water in the kidney tubules and for decreasing urine volume (Dibas et al., 1998). Through vasopressin's actions on the GI tract, more water is also absorbed into the blood through (Olsson, 2005). Restricting daily WI by Katahdin sheep, Boer goats, and Spanish goats from 100 to 40% of ad libitum by 10% in consecutive periods of 2 wk each showed that vasopressin concentrations increased from the baseline level of ad libitum WI (2.3 pg/mL) and were highest (4.3, 6.1, and 8.5 pg/mL in wk 1 and 6.9, 7.8, and 7.7 pg/mL in wk 2) during the most severe water restriction periods of 60, 50, and 40% of ad libitum intake, respectively (Mengistu et al., 2016). In an earlier study (Mengistu et al., 2007a), offering Ethiopian Somali does water daily or 4 d in 4 consecutive periods revealed that plasma vasopressin concentration did not differ between days in each period for the control does (ranging from 1.5 to 3.5 pg/mL). In the water-restricted does, however, vasopressin concentration increased sharply in period 1 (from 1.5 to 10.8 pg/mL) and period 2 (from 2.8 to 10.0 pg/mL), but then decreased on d 4 to less than half the highest concentration of periods 1 and 2 in periods 3 and 4 (4.6 and 4.8 pg/mL, respectively). This drop in vasopressin concentration with time suggests adaption to drinking water shortage as this hormonal response coincided with reductions in plasma osmolality and greater water conservation by the water-restricted goats. In a study by Kaliber et al. (2016), restriction of daily WI by crossbred German Fawn does from 100 to 87, 73, and 56% of ad libitum for 30 d resulted in gradual increases in plasma vasopressin concentrations (12.9, 14.6, 16.1, and 17.4 pg/mL, respectively). These vasopressin levels suggested that the goats did not suffer severe dehydration as evident in mild increases in plasma concentrations of cholesterol, creatinine, glucose, and urea.

Aldosterone, another important hormone for water conservation, is responsible for sodium reabsorption in the kidney and, as a result, stimulates water reabsorption and prevents water loss in the urine (Atlas, 2007; Friis et al., 2013). Increased aldosterone concentrations in plasma or serum have been consistently reported in water restricted sheep. Concentrations of serum aldosterone in Marwari ewes deprived of water for 6 d increased from 18.1 pg/mL during 5 d of ad libitum WI to 24.0, 35.0, and 55.0 pg/mL on d 2, 4, and 6 of water deprivation, respectively, and then decreased to a level (18.8 pg/mL) similar to baseline of ad libitum intake after 72 h of rehydration (Kataria and Kataria, 2007). Plasma aldosterone concentration also increased from 45.2 to 56.7 pg/mL when WI by Malpura ewes was restricted to 60% of ad libitum for 28 d and then returned to a level (47.8 pg/mL) similar to baseline of ad libitum intake within 1 wk of rehydration (De et al., 2015). Notably, the decrease in aldoseterone concentrations during rehydration in both studies reflected inhibition of its secretion as water conservation mechanisms are no longer needed. In contrast, plasma aldosterone concentrations did not differ between wethers having ad libitum access to water or deprived of water for 3 d (averaging 50 pg/mL) under a controlled temperature of 24.8 ^{o}C (Li et al., 2000). The lack of significant effect of dehydration, however, was attributed to that aldosterone concentrations were highly variable among wethers or were below detectable levels.

As the principle stress hormone, cortisol plays an important role in maintaining the balance between body water and electrolytes (Parker et al., 2003). Its concentration, therefore, is important as a stress indicator in all mammals including sheep. Considering that water restriction is a stressful condition, cortisol concentration in blood is expected to increase at the start of drinking water shortage and to subside as the animal becomes better adapted to such a stress. Across the sheep and goats used by Mengistu et al. (2016), plasma cortisol concentration increased from 4.5 ng/mL for ad libitum WI to 5.1, 8.4, 9.6, and 11.8 ng/mL for WI at 70, 60, 50, and 40% of ad libitum, respectively, reflecting the severity of water shortage. Likewise, plasma cortisol concentration in Malpura ewes also increased from 8.1 to 12.6 ng/mL with restriction of WI to 60% of ad libitum and returned to baseline level within 1 wk of rehydration (De et al., 2015). Concentrations of serum cortisol in Marwari ewes deprived of water for 6 d also increased from 6.5 ng/mL during 5 d of ad libitum WI to 9.2, 14.5, and 35.1 ng/mL on d 2, 4, and 6 of water deprivation, respectively, and then decreased to a level (9.8 ng/mL) similar to that on d 2 after 72 h of rehydration (Kataria and Kataria, 2007). The results, however, showed that the ewes needed more than 3 d to recover from the stress that resulted in 6% BW loss, including mild tissue damage, over the 6 d of severe dehydration. In contrast, Li et al. (2000) reported that plasma cortisol concentrations did not differ between wethers having ad libitum access to water or deprived of water for 3 d. Similarly, serum cortisol concentrations were not affected when Awassi ewes were offered water every 3 d for 23 d (Hamadeh et al., 2006), every 4 d for 12 d (Ghanem et al., 2008), or every 4 d for 42 d (Jaber et al., 2004). Aside from the fact that Awassi sheep are known their extreme resilience to drinking water shortage (Laden et al., 1987), it was suggested that when water restriction stress is prolonged, blood cortisol level may be a poor indicator of stress in sheep (Jaber et al., 2004; Hamadeh et al., 2006; Ghanem et al., 2008).

RESILIENCE DIFFERENCES AMONG SMALL RUMINANTS

Species Differences

According to Shkolnik et al. (1980), goats are considered to be more resilient to water restriction than sheep. This generalization, however, was based on anecdotal observations that black Bedouin goats exposed to long droughts in arid regions survived longer than Awassi sheep exposed to the same harsh conditions. Those authors attributed the greater adaptability by goats to their smaller body size and thinner hair coat that allow easier dissipation of heat through the skin. In contrast to other animals where water losses exceeding 15% of BW can be fatal, sheep and Bedouin goats are able to tolerate water losses as high as 20 and 40% of BW, respectively (Shkolnik et al., 1980). This great tolerance to losses of body water is attributed to reliance of sheep and goats, like other ruminants, on the rumen as a water reservoir (Silnikove, 2000a) and their efficient use of physiological mechanisms they have developed to better cope with environmental stressors such as droughts (Parrot et al., 1996; Silanikove, 2000a,b; Chedid et al, 2014). Even though, differences between sheep and goats and among breeds of both species in resilience to limited drinking water availability have been expected, very few studies have made direct comparisons between both species.

Al-Ramamneh et al. (2012) evaluated physiological responses of dry Boer does and dry German black-head mutton ewes to water restrictions of 3 h daily or 6 h every 2 d in 2 consecutive 21-d trials in a temperate climate. No differences in DMI, WI, WI:DMI ratio, or BW between the water-restriction treatments were found for both species, but the sheep had a lower total body water content and higher WI:DMI ratios, rectal temperatures, and respiratory rates than goats. It was concluded, therefore, that both species showed a similar tolerance to a moderate water shortage and that the noted advantages to the goats could be attributed to the important role their hair coat plays in better adaptability to water shortage. In another study, physiological responses of fat-tailed ewes and Kacang does to 50% water restriction with (indoor; 18 to 30 ^oC) or without (outdoor; 18 to 39 ^oC) heat stress were evaluated (Rahardja et al., 2011). Across the different environmental temperatures, water restriction decreased OM intake of chopped native grass (40.9 vs. 50.2 and 42.9 vs. 55.5 g/kg $BW^{0.75}$) and increased OM digestibility (58.0 vs.53.0 and 60.6 vs. 53.9%) by sheep and goats, respectively. Water restriction also decreased plasma volume (57.7 vs. 59.6 and 52.2 vs. 55.9 mL/kg $BW^{0.82}$) and increased plasma PCV (31.3 vs. 29.3 and 36.2 vs. 34.3%) in a similar fashion for sheep and goats, respectively. Both species also maintained similar percentages of the total water lost through urination, defecation, and evaporation. Thus, it was suggested that sheep and goats use different homeostatic strategies for their regulation of body temperature and fluid in their efforts to cope with heat load and water restriction. In another study (Mousa et al., 1983), offering ad libitum access to dry desert grass (containing 3.2% CP on DM basis) to male desert sheep and male desert goats under water restriction of 50% of ad libitum intake decreased DMI by sheep without affecting DM digestibility. In contrast, water restriction did not affect DMI by goats, but increased DM digestibility. Mousa et al. (1983) also reported that water restriction increased serum urea concentration in sheep and goats (15.0 vs. 11.3 and 21.7 vs. 15.3 mg/dL, respectively), decreased hourly urea excretion rate (1.6 vs. 3.5 and 1.5 vs. 3.2 mg/kg $BW^{0.75}$, respectively), and increased urea recycling (87.7 vs. 75.0 and 90.3 vs. 78.7%, respectively). It was concluded, therefore, that desert sheep and goats improved their N metabolism similarly under water restriction. Mengistu et al. (2016) also evaluated the effects of water restriction on performance of male Katahdin sheep and Boer and Spanish goats. Thire results showed that restricting WI to 50% of ad libitum decreased DMI by 30.6, 22.4, and 19.1%, respectively, whereas restricting WI to 40% of ad libitum decreased DMI by 43.8, 34.4, and 35.2%, respectively. These differences in feed intake supported the notion that goats are more resilient than sheep to limited water availability.

Breed Differences

Studies addressing the effects of water restrictions on small ruminant breeds have been limited to goats (Alamer et al., 2006; Qinisa et al., 2011; Mengistu et al., 2016). In the study by Alamer et al. (2006), bucks of the Hipsi, Aardi, and Zumri breeds demonstrated similar resilience to water deprivation for 3 d under temperatures approaching 50 ^{o}C. Measurements of blood components revealed that all breeds activated water conservation mechanisms that included increased rectal temperatures and reduced feed intake, which in turn, drastically decreased BW by 19.6, 22.4, and 19.7% in 3 d, respectively. Qinisa et al. (2011) also demonstrated that offering water daily at 50% of ad libitum intake for 7 d resulted in greater PCV and lower plasma total protein concentration in Tswana than in Boer goats without affecting plasma osmolality or urea concentration. The authors, thus, concluded that both breeds were similarly resilient to drinking water shortage. Mengistu et al. (2016), however, did not report physiological differences between Boer and Spanish goats when their WI was restricted to 90, 80, 70, 60, 50, and 40% of ad libitum intake. Even though sheep are known to be less resilient than goats to environmental stressors (Silanikove, 1994), it is important to note that some sheep breeds are more tolerant than others. For example, Awassi sheep are known for their superior adaptability to semiarid environments where extended drought and high ambient temperatures persist (Laden et al., 1987). However, no direct comparisons between sheep breeds were found.

CONSIDERATIONS FOR IMPROVING RESILIENCE

It is well established that the drastic effects of climate change on animal agriculture are significant and are expected to worsen (Hatfield et al., 2008; Thornton et al., 2009; Misra, 2014). Thus, if the environment itself cannot be controlled, its inhabitants need to become more resilient to the rise in environmental temperatures and expansion of droughts. One way that small ruminants can become resilient is by changing their genetic makeup through crossbreeding and selection programs. According to Thornton (2010), previous practices of selection for production traits such as growth potential and wool production, have indirectly led to decreases in adaptation traits such as decreased expression of genes responsible for vasopressin and aldosterone production. As a result, domesticated sheep and goats have become less efficient at adapting to environmental stressors such as drought and high temperatures. Thus, to produce sheep or goats resistant to drought through genetic selection programs, breeds of each species that are most resilient need to be identified. Within those breeds, superior individual animals from each sex also need to be identified and bred together. After enough generations, offspring may become less affected by harsh climates and possibly continue to produce meat and wool at the levels for which they had been selected. Such improvements in resilience after multiple generations would coincide with the expected expansion of drought and rise in environmental temperatures in the future (Nardone et al., 2010). It is worth noting, however, that those negative expectations about future climate conditions are not absolute and are based solely on recorded climate trends from recent decades.

CONCLUSIONS

As the threats of expansion of drought continue to increase, the health and productivity of small ruminants become major concerns worldwide. Thus, to properly address these concerns, it is essential to establish a database on how different breeds or individuals within breeds of sheep and goats vary in their ability to cope with drinking water shortage. However, despite the fact that the physiological mechanisms of adaptation to limited drinking water availability are reasonably understood, many challenges continue to exist and hinder any progress towards development of resilient animals. In addition to the limited number of water-restriction studies available, other challenges included the use of a limited number of local breeds of sheep or goats, different types of water-restriction strategies, and different experimental designs and conditions that in many cases involved other environmental stressors such as various heat loads and/or poor quality diets. Thus, these challenges not only make it difficult to establish meaningful comparisons among published reports, but also hinder any efforts to develop sheep and goats resilient to drinking water shortage. For those reasons, direct comparisons among breeds of sheep or goats of high resilience potential under controlled conditions are necessary.

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CHAPTER III

EFFECTS OF RESTRICTED AVAILABILITY OF DRINKING WATER ON DRY MATTER INTAKE AND BODY WEIGHT RESPONSES IN HAIR SHEEP BREEDS FROM DIFFERENT REGIONS OF THE UNITED STATES

ABSTRACT

To assess resilience of hair sheep breeds from different U.S. regions to water restriction, 43 Dorper (DOR), 43 Katahdin (KAT), and 44 St. Croix (STC) female sheep with initial body weight (BW) of 60 ± 2.6, 63 ± 2.4, and 45 ± 2.1 kg, respectively, and age of 3.5 ± 0.19 yr were used. The sheep were derived from the Midwest (MW) Northwest (NW), Southeast (SE), and central Texas (TX) with all breeds represented within each of the 4 climatic regions. In 4 separate trials using different sets of sheep in the spring and summer of 2016 and 2017, the sheep were housed individually and fed a pelleted diet at 160% of the metabolizable energy requirement for maintenance. In each trial, all sheep were offered water ad libitum for 2 wk (period 1), 75% of ad libitum intake for 2 wk (period 2), and 50% of ad libitum intake for 5 wk (period 3) at 0730 h and were weighed 3 times each week at 1300 h. Data from the 4 trials were pooled and analyzed for effects of and interactions involving breed, region, period, and week within period for dry matter intake (DMI), water intake (WI), and BW. In period 3, there were

breed × region × week interactions for BW and DMI expressed as g/d, % of BW, and g/kg $BW^{0.75}$. The interaction in BW was mainly because of relatively low values for KAT from the MW and to a lesser extent the NW compared with more similar values among regions for DOR and STC and smaller differences among weeks for KAT from the MW and NW. Also in period 3, DMI decreased slightly from wk 1 to 2, then increased except for continuing decline to wk 4 for KAT from the MW and to a lesser degree for DOR from the NW. Change in average daily gain during period 3 was not influenced ($P > 0.05$) by interactions but differed ($P < 0.05$) among weeks, with weight loss in wk 1 being fully compensated for in wk 2, 3, 4, and 5 (-109, 35, 83, 64, and 152 g/d, respectively; SEM = 18.0). In conclusion, water restriction at 50% of ad libitum intake by individual sheep in the absence of heat stress conditions while offering feed above the maintenance requirement showed no clear differences among DOR, KAT, or STC in tolerance to limited drinking water availability based on BW and DMI responses. Each breed, however, appeared highly resilient.

Keywords: body weight, feed intake, hair sheep, resilience, water restriction

INTRODUCTION

In recent years, rising temperatures and expansion of droughts due to climate change represent major threats to animal agriculture in developing (Thornton et al., 2009; Sejian, 2013; Misra, 2014) and developed countries, including the U.S. (Hatfield et al., 2008). In a USDA report on climate change, Hatfield et al. (2008) addressed the severe production losses to animal agriculture in the U.S. due to adverse environmental stressors, attributed those losses to increased maintenance requirements for sustaining body temperature and to decreased feed intake under rising temperatures, and emphasized prior conditioning to such stressors as a critical strategy to minimize catastrophic economic losses. However, conditioning of ruminants to survive, thrive, and possibly produce at levels matching their genetic potential while tolerating high environmental temperatures and droughts would require efficient use of genetic diversity for selection and development of resilient animals. For ruminants, this approach would rely on existing variation among breeds in tolerance to harsh environmental conditions such as high temperatures (Brown et al., 1988; Silanikove, 2000a; Gaughan et al., 2010) and droughts (Khan et al., 1978; Igbokwe, 1993; Hossaini-Hilali et al., 1994).

Even though water is the single most important nutrient required by ruminants and other animals to support health and production through essential physiological functions, studies on how ruminants respond to its availability have been limited. Those studies have focused mostly on sheep (Aganga et al., 1989; Hamadeh et al., 2006; Kumar et al., 2016) and goats (Alamer, 2006; Mengistu et al., 2007a; Kaliber et al., 2016) adapted to arid or semiarid regions where availability of drinking water has been a persistent problem due to high temperatures and severe droughts. Hair sheep are examples of ruminants not only well adapted to the adverse climates of arid and tropical regions, but also superior in fertility, survivability, and production of meat to many wool sheep raised under similar conditions (Bradford et al., 1983; Bunge et al., 1993; Wildeus, 1997). They also produce better quality skins (Bradford et al., 1983), exhibit more resistance to gastrointestinal parasites (Burke and Miller, 2004), have higher feed efficiency (Bunch et al., 2004), and are better in utilizing low or moderate quality forages than wool sheep (Silva et al., 2004; Wilkes et al., 2012). For these reasons, almost 70% of the sheep population in Mexico, for example, are hair sheep breeds (Sánchez-Dávila et al., 2015) and many of those breeds are becoming more popular worldwide. Of those, Dorper (DOR), Katahdin (KAT), and St. Croix (STC) are major hair sheep breeds in the U.S. (Thomas, 1991).

Although hair sheep breeds are expected to vary in their resilience to environmental stressors such as droughts, no published reports involving direct comparisons of hair sheep breeds under controlled experimental conditions were found. Moreover, it is unclear whether sheep from the same breed raised in different climatic regions would exhibit similar resilience to limited drinking water availability. Therefore, the objective of this study was to evaluate responses in body weight (BW) and intakes of feed and water to limited drinking water offered to DOR, KAT, and STC sheep originating from 4 distinct climatic regions of the U.S.

MATERIALS AND METHODS

Animals and Treatments

The protocols for this experiment were approved by the Langston University Animal Care Committee. Forty-three DOR (initial BW = 60 ± 2.6 kg), 43 KAT (63 ± 2.4 kg), and 44 STC (45 ± 2.1 kg) sheep (3.5 ± 0.19 yr old) were used. The sheep were obtained from 45 commercial farms in the Midwest (MW; Iowa, Minnesota, Wisconsin, and Illinois), Northwest (NW; mainly Oregon and 2 farms in Washington), Southeast (SE; mainly Florida and 1 farm in southern Georgia), and central Texas (TX) regions of the U.S. and were used in a repeated measures experiment (Kuehl, 1999). The experiment consisted of 4 separate trials using 4 different sets of sheep that occurred in the spring (January-April) and summer (June-August) of 2016 and the spring (January-April) and summer (July-September) of 2017.

The 4 regions were chosen for their different climatic conditions using data from various computer programs such as Geographic Information System (GIS; Environment Rating Scales Institute, Redlands, CA) and National Ecological Observatory Network domains (NEON, Battelle Memorial Institute, Columbus, OH). The sheep breed associations for DOR, KAT, and STC were contacted, the zip codes of their members were geocoded (a process of converting addresses into geographical coordinates), and the geocoding for each breed was overlaid into the online NEON domains that were based on climate and geographical factors. Of the farms from which the sheep were obtained, one producer had two separate flocks and two had sheep of 2 breeds of different flocks. Before the onset of each trial, the sheep were vaccinated against clostridial organisms with Covexin® 8 (Schering-Plough Animal Health, Kenilworth, NH). The FAMACHA© score (van Wyk and Bath, 2002) determined at that time did not suggest a need for treatment for internal parasites. The sheep were housed in a well-ventilated room individually in 1.05 × 0.55 m elevated pens with a plastic–coated expanded metal floor and each pen was fitted with a plastic barrel for feed and a bucket for water. Fecal and urinary excretions were removed and an odor absorbent was dispensed on the floor under pens daily.

Weather data were obtained from the Oklahoma Mesonet Guthrie station. The Oklahoma Mesonet, a network of environmental monitoring stations across Oklahoma, is maintained by the University of Oklahoma and Oklahoma State University. Mesonet measures air temperature and relative humidity at 1.5 m above ground using a thermistor-sortion probe (Campbell Scientific, Inc., Logan, UT) as described by Brock et al. (1995). Data downloaded were hourly temperature and relative humidity conditions at Langston

University for the dates of each of the 4 trials of the experiment. These data were used to calculate heat load index (HLI) according to Gaughan et al. (2010): HLI = 8.62 + (0.38 × RH) + (1.55 × BG) – (0.5 × WS) + $e^{(2.4 - WS)}$, whereas RH = relative humidity (%), BG = black globe temperature (ºC), WS = wind speed (m/s; assumed zero), and e = base of the natural logarithm. Those data were also used to calculate the temperature-humidity index (THI) according to Amundson et al. (2006): THI = (0.8 × ºC) + (RH/100) × (ºC − 14.4) + 46.4. Averages for temperature, RH, HLI, and THI outside the animal room were summarized across the 4 trials for the 3 experimental periods of drinking water availability and are presented in Table 1. The temperature and RH inside the animal room were also recorded every 1 h using a temperature and humidity monitor (Hobo®Temperature/RH Data Logger, model number U12-011; Onset Computer Corp., Bourne, MA). The temperature and RH records for the second trial (summer of 2016), however, were lost due to a malfunction of the instrument used. Thus, averages for temperature, RH, HLI, and THI inside the animal room were summarized across the 3 remaining trials and presented in Table 1.

The sheep were fed a pelleted diet (Table 2) at 71 grams of dry matter (DM) per kg of metabolic body weight ($BW^{0.75}$) to meet approximately 160% of the metabolizable energy requirement for maintenance (NRC, 2007). There were two daily meals of equal amounts at 0800 and 1500 h, but the time of feeding on Wednesday mornings was 1 h later due to collection of blood samples before feeding. The amounts of feed offered were recorded and orts were weighed daily at 0800 h and used to calculate daily DM intake (DMI) by each animal. All sheep were weighed 3 times weekly (Monday, Wednesday, and Friday) at 1300 h to monitor change in BW throughout each trial. After weighing, half of the sheep were allowed access to an open floor area for 2 h before returning to their pens, an arrangement that provided an average of 3 h of group socialization each week.

The first 2 wk of each 9-wk trial served as a baseline period (period 1) during which time all sheep had free access to water. Ad libitum water intake (WI) was determined by filling the water buckets to capacity twice daily (0700 h and 1500 h) and weighing the remaining water at 0600 h the following day. Average WI by each animal over the 2-wk baseline period was then used as the estimate of ad libitum intake. Following the baseline period, all animals were offered water at 75% of ad libitum intake for 2 wk (period 2). Water was offered once daily at 0730 h and was consumed in a relatively short time. Next, water was restricted to 50% of ad libitum intake for 5 wk and was offered once daily at 0730 h (period 3). During this period, the sheep were expected to adapt to this restriction by conserving more water. At the end of those 5 wk, the sheep entered a rehydration phase by gradually bringing WI back to ad libitum by increasing the amount offered by 10% of ad libitum intake every 2 d and offering the water in 4 equal portions throughout the day (i.e., 0730, 0830, 1430, and 1530 h) to prevent hemolysis.

The protocol used for dehydration and rehydration of the sheep and selection of the water restriction treatments were based on the results of an initial study in our laboratory where the effects of restricting WI by KAT sheep and Boer and Spanish goats to 90, 80, 70, 60, 50, and 40% of ad libitum for 1 or 2 wk each were evaluated (Mengistu et al., 2016). Because there were minor physiological response differences (e.g., cortisol concentration) or no differences between the 50% and 40% restriction levels, the 50% of ad libitum WI was determined as an appropriate level for maximum water restriction in evaluations of resilience to limited water availability. It was also determined that a length of 2 wk rather than 1 wk for a water restriction level would be more appropriate in terms of increasing the meaningfulness of the measurements evaluated, especially BW.

Sample Collection and Analysis

Representative samples of the pelleted diet were collected daily and stored at room temperature. Weekly composite samples were formed and ground to pass through a 1-mm screen and analyzed for DM and ash (AOAC, 2006), nitrogen (Leco TruMac CN, St. Joseph, MO), gross energy using a bomb calorimeter (Parr 6300; Parr Instrument Co. Inc., Moline, IL), and neutral detergent fiber (Van Soest et al., 1991) using an ANKOM200 Fiber Analyzer (filter bag technique; ANKOM Technology Corp., Fairport, NY).

Statistical Analysis

Data were analyzed with mixed effects models using the MIXED procedure of SAS (Littell et al., 1996; SAS, 2013). Different statistical models were used for different response variables and each response variable was analyzed in multiple ways. To analyze responses in BW, DMI, and WI during the baseline period, the model included the fixed effects of set, breed, region, and the breed × region interaction with animal considered as a random effect and age as a covariate.

To analyze changes in BW, DMI, and WI across the 3 experimental periods, the model contained the fixed effects of set, breed, region, period, week within period, breed × region, breed × period, breed × week, region × period, region × week, period × week, breed × region × period, breed × region × week, breed × period × week, region × period ×

week, and the 4-way interaction of breed × region × period × week with animal considered a random effect and age as a covariate. For this analysis, only the first 2 wk of data in period 3 were used so that periods were of the same length.

To assess differences in BW, DMI, and WI across the 5 wk of period 3, the model included set, breed, region, week, breed × region, breed × week, region × week, and breed × region × week as fixed effects and animal as a random effect. Animal age and initial values taken during period 1 (baseline) also served as covariates in the model. Average daily gain (ADG), calculated by regression analysis (REG procedure of SAS), was also assessed in the 5 wk of period 3. To accomplish this, BW values from Monday, Wednesday, and Friday of each wk and Monday of the subsequent wk (4 BW values) were used to estimate weekly ADG values. This method of calculating ADG was preferred because BW was measured 3 times each wk.

An average for each response variable was taken during the last 2 wk of period 3 because this was when animals were expected to be adapted to limited water availability. The model for analyzing sources of variation in BW, DMI, and WI during these last 2 wk included set, breed, region and the breed × region as fixed effects and animal as a random effect with age and baseline values being used as covariates.

Means were separated using the LSMEANS statement and pairwise comparisons were conducted using Fisher's LSD (PDIFF option). Statistical significance was declared at $P < 0.05$. It is worth noting that the U.S. populations of the hair sheep breeds used in this study were adequately represented because they were obtained from 4 distinct regions with different climatic conditions. Nevertheless, because the number of sheep per breed and region was limited and not exactly equal, breed × region interaction means were presented to primarily explain variability within breed with much greater attention given to the main effect of breed than region.

Spearman's rank correlation coefficients (*sr*) were determined using the CORR procedure of SAS to evaluate consistency in the ranking of response variables among the 3 periods and among the 5 wk of period 3 within each hair sheep breed and overall for DMI in g/d. To assess variability among breeds for each response variable during the last 2 wk at 50% water restriction, Bartlett's test for homogeneity of variance was performed using the GLM procedure of SAS.

RESULTS AND DISCUSSION

Resilience to Limited Water Availability

Many water restriction studies have been conducted using different breeds of sheep (Aganga et al., 1989; Hamadeh et al., 2006; Kumar et al., 2016) and goats (Alamer, 2006; Mengistu et al., 2007a; Kaliber et al., 2016) native to arid and semiarid regions to identify the physiological mechanisms small ruminants have developed to cope with pervasive high temperatures and droughts (Parrot et al., 1996; Silanikove, 2000b). Elucidation of such mechanisms is needed for selection of animals more tolerant to shortages in drinking water and for improved management. In recent years, however, the adverse weather conditions caused by climate change have made this need a high priority considering that hotter weather conditions and severe droughts have been spreading worldwide (Hatfield et al., 2008; Sejian, 2013; Misra, 2014).

Studies evaluating tolerance of sheep and goats to water shortages have varied in their approach, with the majority testing infrequent watering regimes. Using Awassi ewes, a fat-tailed Middle Eastern breed, water was offered ad libitum daily versus every 3 d (Hamadeh et al., 2006), every 2 or 4 d (Jaber et al., 2004), or every 4 d (Ghanem et al., 2008). With Ethiopian Somali goats, water was offered ad libitum daily versus every 4 d to does (Mengistu et al., 2007a) and every 2, 3, or 4 d to bucklings (Mengistu et al., 2007b). In another study, bucks of the Saudi Arabian breeds of Hipsi, Aardi, and Zumri were given ad libitum access to water for 1 d, deprived of water for 3 d, and rehydrated for 1 d (Alamer, 2006). Those studies were designed to reflect practices in arid and semiarid regions where animals travel long distances in search of feed and water that are naturally scarce under harsh environments. For practical implications, those studies also used local breeds known for their ability to survive for a few days under heat stress and without access to drinking water. However, the resilience unique to such breeds makes the infrequent watering regimes tested in those studies possibly impractical and potentially dangerous to breeds adapted to less harsh or temperate environments.

In other studies evaluating tolerance of sheep and goats to water shortage in arid and semiarid regions, restriction was accomplished by offering water every day in amounts less than ad libitum intake. Examples included offering water at 80 or 60% of ad libitum intake to Malpura ewes (De et al., 2015) or lambs (Kumar et al., 2016) and at 50% of ad libitum intake to growing Baluchi lambs, another fat-tailed Middel Eastern breed (Vosooghi-Postindoz et al., 2018). Using goats, water was offered at 75 or 50% of ad libitum intake to Aardi does (Alamer, 2009) and at 87, 73, or 56% of ad libitum intake to crossbred German Fawn does (Kaliber et al., 2016). In studies conducted in temperate climates, water was offered to control groups ad libitum versus at 80 or 60% of WI by the controls to Comisana ewes (Casamassima et al., 2008) and Lacaune ewes (Casamassima et al., 2016, 2017). Most of those studies, however, did not provide explanations for how the levels of water restriction or their durations were selected. Nevertheless, this approach to water restriction seems more practical, carries less risks to the health and production of small ruminants subjected to shortage of drinking water, and could be used as a viable alternative to infrequent watering.

The watering protocol for the present study, especially the levels and durations of water restriction in each period, was based on the results of an initial study with KAT sheep and Boer and Spanish goats offered water at 100, 90, 80, 70, 60, 50, and 40% of ad libitum intake for 1 or 2 wk each (Mengistu et al., 2016). First, lower plasma concentrations of vasopressin in wk 1 than wk 2 for animals at the 60 and 40% restriction levels suggested a length of at least 2 wk at a given water-restriction level as more appropriate than 1 wk. This finding was supported by a literature review on sheep response to water stress in arid environments, which emphasized the role of vasopressin in improving water economy through the kidneys and the gastrointestinal tract by decreasing urine output and producing dry feces (Chedid et al., 2014). Second, it was extrapolated from the data that extending the test restriction period to more than 2 wk may increase the meaningfulness of BW as a practical measure to evaluate differences among sheep and goats in resilience to drinking water shortage. It is expected, however, that the likelihood of BW being a good predictor of resilience is less with mature than younger, growing animals. Third, minimizing the water restriction steps leading to the lowest test level seemed feasible. Fourth, higher plasma concentrations of cortisol in animals restricted to 40 than 50% of ad libitum WI combined with marked reductions in DMI by some in wk 2 at those levels suggested the appropriateness of a maximum restriction level of 50%. For those reasons, the present study was designed to offer the sheep water at 100, 75, and 50% of ad libitum intake in 3 sequential periods lasting 2, 2, and 5 wk, respectively.

Experimental Considerations

Generally, THI is the most effective and commonly used index to evaluate effects of heat stress on ruminants as it considers the impacts of ambient temperature and relative humidity (Gaughan et al., 1999; Nasr and El-Tarabany, 2017). Hahn et al. (2009) considered a THI of ≤ 74 as a comfort threshold for beef cattle, above which heat stress can be alarming and even dangerous at THI ≥ 84. Nevertheless, negative effects on reproductive performance of beef cattle were detected at THI > 68 and exacerbated at higher THI values (Amundson et al., 2006). In a review of published studies on the effects of heat stress on dairy cattle in temperate zones, Silankove and Koluman (2015) also identified a THI < 65 as a comfort threshold, beyond which animals begin to suffer grave consequences to their health and production. Years earlier, Vitali et al. (2009) demonstrated that mortality in a dairy herd was minimum at THI of 70 and maximum at 87. As to hair sheep breeds other than those used in the present study, Seixas et al. (2017) demonstrated that in Brazil, Santa Inês and Morada Nova sheep were thermally comfortable at THI averaging 59 and 61 but suffered heat stress at higher THI values such as 79. In our laboratory, KAT sheep were shown to be in thermal comfort at THI of 64.5 and at HLI, another heat stress index, of 66 and began to exhibit signs of heat stress at THI > 74 and HLI > 75 (Mengistu et al., 2017). In the present study, the results (Table 1) for outside (across the 4 trials) and inside (across 3 trials) the room where the sheep were kept showed that THI ranged from 43.3 to 48.5 and from 45.1 to 46.4, respectively, whereas HLI ranged from 69.0 to 73.2 and from 70.4 to 74.3, respectively. These results demonstrated that heat stress was not a factor as our sheep were within their comfort threshold. In addition to assuring comfort of the sheep used in the 4 trials, possible confounding factors concerning performance were also avoided. Thus, the sheep were neither pregnant nor lactating and had ad libitum access to a balanced diet that met and exceeded their maintenance requirements (NRC, 2007).

Baseline Period

This study was unique in that it was the first to directly compare responses of different sheep breeds from different climatic regions to limited drinking water availability. When water was offered ad libitum during the 2-wk baseline period, no significant breed × region interactions were detected for BW, DMI, or WI (Table 3). Thus, main effect means are presented in Table 4. Neither the breed nor the region affected ($P > 0.05$) DMI, WI, or the WI:DMI ratio. Initial BW was similar ($P > 0.05$) for DOR and KAT sheep averaging 61.4 kg, which was 32% greater ($P < 0.05$) than BW of STC. This could be attributed to the fact that both breeds are heavier and have a larger mature size than other hair sheep, including STC (Burke and Apple, 2007; Wildeus et al., 2007; López-Carlos et al., 2010). As to the effect of region, the sheep from the NW had greater ($P < 0.05$) BW than those from the SE or TX, which could be attributed to the cool, wet climate under which they had been raised. It could also be possible that sheep native to the NW climate deposit more fat as an adaptive mechanism to insulate heat in their body and help maintain thermoneutral conditions during winter. It is well established that when humidity is relatively high, as is the case in the NW region, evaporative heat loss is reduced (Finch, 1985).

In most studies evaluating resilience to limited drinking water availability, the level of restriction was not based on ad libitum WI (baseline) by the same sheep (Casamassima et al., 2008, 2016; Kumar et al., 2016) or goats (Kaliber et al., 2016). Instead, the restricted levels were determined as proportions of WI by groups of similar animals having ad libitum access to water. This arrangement does not consider actual ad libitum intake by the animals being subjected to water restriction (i.e., individual animal variability), which could influence the results and their interpretation. In contrast, the present study was designed to include a 2-wk baseline period during which all sheep were offered water ad libitum and both the initial and final restriction levels used (75 and 50%, respectively) were determined for each sheep based on its own ad libitum WI. Moreover, in order to assess change in BW, DMI, and WI across the 5 wk of period 3 with the 50% water restriction level, the initial values obtained during the baseline period along with animal age served as covariates in the statistical model used to evaluate resilience.

Period Comparisons

The *P* values for the main effects of and interactions among breed, region, period, week within period, animal set, and age as to BW, DMI, WI, and the WI:DMI ratio are presented in Table 5 with the corresponding means in Table 6 and Fig. 1 to 8. Consistent with the experimental design of the study, daily WI (data not shown) was greatest ($P < 0.05$) when the sheep had ad libitum access to water and decreased ($P < 0.05$) in the two restriction periods of 75% and 50% of ad libitum (3,543, 2,620, and 1,779 g for periods 1, 2, and 3, respectively; SEM = 54.1).

No significant 4-way interactions were detected for any of the measurements evaluated, but there were significant 3-way interactions for WI and 2-way interactions for

BW and WI Table 5). Three significant breed × region × period interactions are presented in interaction plots for WI as a % of BW, in g/kg $BW^{0.75}$, and relative to DMI in Fig. 1, 2, and 3, respectively. In each period, WI as a % of BW and in g/kg $BW^{0.75}$ was greater ($P <$ 0.05) for KAT sheep from TX than KAT from the other regions, which had similar ($P >$ 0.05) intakes (Fig. 1 and 2; Panel B) and regardless of the region, DOR and STC sheep had similar ($P > 0.05$) WI (Fig. 3 and 4; Panels A and C). Across regions and periods, however, the WI:DMI ratio was highest ($P < 0.05$) for KAT sheep from TX (Fig. 3; Panel B) while DOR and STC were not affected ($P > 0.05$) by region as they had similar ($P >$ 0.05) ratios in each period (Fig. 3; Panels A and C).

As to the 2-way interactions, a significant breed × period interaction showed WI in g/d to be highest ($P < 0.05$) for KAT sheep, lowest ($P < 0.05$) for STC, and intermediate for DOR in period 1 only with no clear trends in each of the remaining periods (Table 6). Another significant breed × period interaction for WI as a % of BW also showed no clear trends in periods 1 and 2, but revealed similar ($P > 0.05$) intakes in period 3 (Table 6). Notably, the breed × period interaction means for most response variables in those interactions were somewhat inconsistent with breed means presented for period 1 alone (Table 4). These inconsistencies were due to greater variability when analyzing period 1 data alone versus with periods 2 and 3 data included and the resulting adjustments from using LSMEANS in SAS. A significant region × period interaction revealed that BW increased from period 1 to period 2, with greater ($P < 0.05$) change for sheep from TX (Fig. 4). Conversely, BW decreased from period 2 to period 3, with the decline greatest ($P < 0.05$) for those from the MW. Another significant region × period interaction revealed that in each of the 3 periods, WI in g/d was similar ($P > 0.05$) for sheep from the NW and TX, lowest (*P* < 0.05) for sheep from the SE, and intermediate for sheep from the MW (Fig. 5). The fact that sheep from the NW, SE, and TX lost less BW than those from the MW between periods 2 and 3 suggests that hair sheep previously adapted to the climates of those regions may have higher resilience to environmental stressors such as drought (e.g., restricting WI to 50% of ad libitum) than those from the MW.

Significant 2-way interactions were also found between period and week within period for BW, DMI expressed as g/d, % of BW, and g/kg $BW^{0.75}$, and the WI:DMI ratio (Fig. 6 to 8). The factor most responsible for the interaction for BW was a greater (*P* < 0.05) value in wk 2 vs. 1 of period 1 as the values were similar (*P* > 0.05) between weeks in periods 2 and 3 (Fig. 6). The interactions for DMI also resulted from greater (*P* < 0.05) values in wk 2 vs. 1 in period 1, no differences (*P* = 0.693) in period 2, and lower (*P* < 0.05) values in wk 2 vs. 1 in period 3 (Fig. 7). Finally, the period × week interaction for the WI:DMI ratio was characterized by similar (*P* = 0.409) ratios between weeks in period 2, lower (*P* < 0.05) ratio in wk 2 vs. 1 in period 1, and numerically (*P* = 0.068) greater ratio in wk 2 vs. 1 in period 3 (Fig. 8). The interactions in Fig. 7 infer that feed intake by sheep was affected by the different water restriction treatments and that the amount of feed consumed did not stay the same for each week within each period. As a result, these differences in DMI between weeks within each period was the primary driver of the interaction in Fig. 8 because the amount of water offered each week did not change within each period. In contrast to these results, there were no significant period × week interactions for total DMI or hay DMI in the study by Mengistu et al. (2016) when KAT wethers were subjected to progressive water restriction at 90, 80, 70, 60, 50, and

40% of ad libitum intake for 2 wk each. However, due to the different experimental designs used in both studies, it is difficult to make period × week comparisons.

Table 6 summarizes the means for significant main effects not involved in interaction as well as the means for a significant breed × period interaction for WI in g/d and as a % of BW. When averaged across the three periods, DOR and KAT sheep had similar ($P > 0.05$) BW and DMI in g/d that were greater ($P < 0.05$) than those for STC. However, the difference in BW was relatively greater than that for DMI in g/d, causing DMI as a % of BW to be greatest ($P < 0.05$) for STC. There were no differences ($P > 0.05$) among breeds for DMI in g/kg $BW^{0.75}$, WI in g/kg $BW^{0.75}$, or the WI:DMI ratio. But when WI was expressed as a % of BW, the three breeds had similar ($P > 0.05$) intakes during each period that averaged 6.57, 4.75, and 3.25% (SEM = 0.204) for 100%, 75%, and 50% of ad libitum intakes, respectively.

Notably, most studies using performance of small ruminants as an indicator of tolerance to drinking water shortage have consistently demonstrated decreases in DMI and BW during water restriction, with the magnitude of the response usually reflecting the severity of the dehydration tested. Restricting daily WI of Aardi does to 75 and 50% of ad libitum intake over 6 d was shown to decrease DMI by 14 and 22% and BW by 6 and 8%, respectively (Alamer, 2009). This rapid decline in performance in less than a week was attributed, in part, to the hot summer of Saudi Arabia that approached 50 ^{o}C and seemed to have exacerbated the adverse effects of water shortage. Moreover, when Baluchi lambs were offered water low or high in total dissolved solids at 100 or 50% of ad libitum intake over 6 wk, water restriction decreased DMI by 40 and 42% and ADG by 64 and 75%, respectively (Vosooghi-Postindozet al., 2018). Offering water to Awassi ewes in a temperate climate every 2 or 4 d also decreased DMI by 24 and 44% and resulted in weight loss of 0.84 and 3.32 kg over 6 wk, respectively (Jaber et al., 2004). Though BW change was not reported, offering Lacaune ewes water at 80 or 60% of ad libitum intake in a temperate climate also decreased DMI by 16 and 36%, respectively, by the end of a 4-wk trial (Casamassima et al., 2016). In determining the appropriate level of maximum water restriction to be used in the present study, Mengistu et al. (2016) reported reductions in DMI that reached 30.6 and 43.8% for KAT sheep, 22.4 and 34.4% for Boer goats, and 19.1 and 35.2% for Spanish goats when their WI decreased gradually by 10% from 100% to 50 and 40% of ad libitum, respectively. Across species, BW also decreased from 27.5 and 26.5 kg when animals were offered water ad libitum for 1 or 2 wk to final weights of 24 and 23 kg, respectively, when water was restricted to 40% of ad libitum intake.

A drastic decline in BW of does (Alamer, 2009) and ADG of lambs (Vosooghi-Postindozet al., 2018) were reported when the 50% water restriction level used in the present study was tested. In those studies, gradual restriction of WI by sheep and goats to 50% of ad libitum intake, however, resulted in moderate losses ranging from 12.7 to 13.2% of their BW when offered water ad libitum. In contrast, our sheep regardless of their breed or region gained weight when water availability was switched to 75% of ad libitum for 2 wk (period 2) and minor BW losses occurred (ranging from 0.69 to 1.52% of their BW) when water was restricted to 50% of ad libitum for 2 wk (period 3). These minor changes in BW suggest a high degree of resilience to drinking water shortage. As to the different magnitudes of impact the 50% water restriction level had on BW in the present study versus those of Alamer (2009) and Vosooghi-Postindozet al. (2018), it is evident that the variable responses could be attributed, in part, to animal and weather differences. We used mature sheep at maintenance versus lactating does or growing lambs, respectively. The environmental temperatures under which the water-restricted animals were kept also varied and ranged between 13.6 and 21.3 ^{o}C in the present study, approached 50 ^{o}C in that of Alamer (2009), and ranged between 34 and 37 ^{o}C in that of Vosooghi-Postindozet al. (2018). The differences in BW response in the present study and that of Mengistu et al. (2016) could also be attributed, in part, to the use of younger animals (averaging 1-yr old) that were kept under higher environmental temperatures (ranging between 19.1 and 29.8 ^{o}C) in the earlier study.

In some studies using small ruminants in temperate climates, DMI was not affected by restricting water availability. Examples include offering water at 80 or 60% of ad libitum intake to Comisana ewes (Casamassima et al., 2008). Similarly, DMI by crossbred German Fawn does was not altered by restricting WI to 87 or 73% of ad libitum but decreased when the water restriction level reached 56% of ad libitum intake (Kaliber et al., 2016). This observation suggests that there is a threshold that needs to be reached before a shortage in water availability affects feed intake. This threshold, however, is expected to vary and be influenced by weather conditions, animal factors, and the diet. As to the latter, restricting WI by desert goats to about 40% of ad libitum tended to decrease DMI of good and poor quality hays by 19 and 21%, respectively (Ahmed and El Kheir, 2004).

Some water restriction studies suggested a mechanism by which ruminants compensate for reduced feed intake, including increased nutrient digestibility as a result of increased digesta retention time in the rumen. For example, Silanikove (1985) showed that restricting WI by desert and non-desert goats from ad libitum each day to every 2 or 3 d decreased DMI in the water restriction treatments from 63.9 to 54.9 g/kg$^{0.75}$ and from 95.0 to 59.5 g/kg$^{0.75}$, respectively, while DM digestibility of alfalfa hay increased from 71.6 to 74.1% and from 66.8 to 71.2%, respectively. Nejad et al. (2014), however, showed that restricting water availability to Corriedale ewes from ad libitum throughout the day to 2 h daily did not alter DMI but increased digestibility of organic matter and neutral detergent fiber by 4.0 and 6.6 percentage units, respectively. In a study of Senn et al. (1996), depriving lactating cows of drinking water for 48 h was shown to decrease BW and DMI by 12 and 23%, respectively, and the latter was attributed to reduced meal size. The same group later established that reduced meal size was a mechanism the cows used to cope with abnormal increases in rumen fluid osmolality during water restriction (Steiger Burgos et al., 2000). Exploring if other mechanisms through digestion or metabolism are activated by water restriction to 75 or 50% of ad libitum intake over 8 d revealed that the cows compensated for decreased DMI at the 50% restriction level by decreasing milk production, increasing digestibility of organic matter, and improving efficiency of energy use, including a decrease in heat production and energy needs for maintenance (Steiger Burgos et al., 2001). It is extrapolated, therefore, that the resilience of the hair sheep used in the present study from restricting WI to 50% of ad libitum was possibly a combination of efficient use of the limited water available and improvement in digestion and utilization of the reduced feed consumed.

Weekly Changes During Period 3

The *P* values for BW, DMI, WI, and the WI:DMI ratio during the 5 wk of period 3 are presented in Table 7. There were significant 3-way interactions among breed, region, and week for BW, DMI expressed as g/d, % of BW, and g/kg $BW^{0.75}$, and the WI:DMI ratio that are presented in Fig. 9 to 13. The interaction for BW (Fig. 9) was mainly attributable to greater differences among regions for KAT sheep, with either numerically ($P \leq 0.142$) or statistically ($P < 0.05$) lower values in most weeks for the MW region and numerically lower values for the NW versus SE ($P = 0.195$) and TX ($P = 0.067$). Moreover, other than a change between wk 4 and 5, there was less change in BW for KAT sheep from the MW and NW than for other breeds or regions. The breed × region × week interactions for all expressions of DMI (Fig. 10, 11, and 12) also appeared largely due to values for KAT sheep from the MW and DOR from the NW as well. Notably, DMI in most cases differed little among weeks, but values for KAT sheep from the MW and DOR from the NW decreased until wk 4 and increased slightly thereafter. Because there was no breed × region × week interaction for WI in g/d ($P = 0.230$; Table 7), the significant 3-way interaction detected for the WI:DMI ratio reflected the unique aforementioned pattern of change in DMI by KAT sheep from the MW and DOR sheep from the NW (Fig. 13).

There were significant 2-way interactions between breed and week for WI as a % of BW (Fig. 14; Panel A) and in g/kg $BW^{0.75}$ (Fig. 14; Panel B) that could be explained by the lowest WI for STC sheep relative to the other breeds in wk 4 and wk 5. Because WI in g/d was the same each week, the differences were due to numerical ($P = 0.445$) changes in BW for DOR (56.7, 56.2, 56.7, 57.1, and 57.8 kg), KAT (56.6, 56.2, 56.7, 57.0, and 57.9 kg), and STC (55.6, 55.7, 56.2, 56.8, and 57.3 kg) in wk 1, 2, 3, 4, and 5, respectively. There were also significant region × week interactions for WI as a % of BW (Fig. 15; Panel A) and in g/kg $BW^{0.75}$ (Fig. 15; Panel B) that could be explained by numerically lower ($P > 0.05$) intake by sheep from the SE and TX than those from the other regions in wk 3 forward. Again, because WI in g/d was the same each week, the differences were due to numerical ($P = 0.066$) changes in BW for sheep from the MW (56.3, 55.8, 56.3, 56.5, and 57.5 kg), NW (56.0, 55.8, 56.0, 56.3, and 57.0 kg), SE (56.1, 56.0, 56.7, 57.3, and 58.1 kg), and TX (56.7, 56.5, 57.1, 57.6, and 58.1 kg) regions in wk 1, 2, 3, 4, and 5, respectively. Finally, Table 8 included main effects means for breed as to all measurements ($P > 0.05$) and for week as to ADG, which was not influenced ($P > 0.05$) by any 3-way or 2-way interactions (Table 7). Across breeds and regions, loss of BW occurred in wk 1 and ADG was positive in wk 2, 3, 4, and 5, being greatest ($P < 0.05$) in wk 5.

The resilience of our sheep to water restriction was displayed in their performance while their WI was restricted to 50% of ad libitum for 5 wk. The breed × region × week interaction plots for period 3 data analyzed alone showed that regardless of breed or region, BW of most sheep was either stable or decreased in wk 1 and gradually increased throughout the remaining weeks (Fig. 9). Calculations of ADG across breeds and region showed that the sheep lost weight in wk 1, gained modest weight in wk 2, 3, and 4, and gained even more in wk 5 (Table 8). Expressing the BW change for each week as a proportion of average BW of the 3 hair sheep breeds (56.7 kg; Table 8) revealed that the sheep lost 1.4% of BW in wk 1 and gained 0.4, 1.0, 0.8, and 1.9% of BW in wk 2, 3, 4, and 5, respectively. Considering that DMI did not markedly change from week to week in period 3, the weight gain detected could be due to greater DM digestibility and improved efficiency of energy utilization (Steiger Burgos et al., 2001) in period 3 than in periods 1 and 2, reflecting full adaptation to water restriction as week advanced. The results suggest that the reductions in DMI due to water restriction at 50% of ad libitum intake were not severe enough to adversely affect BW, considering that the sheep had ad libitum access to a balanced diet at a level designed to meet and exceed their nutrient requirements for maintenance. The continuous increase in BW for all sheep between wk 2 and 5 of water restriction also suggests that the first 2 wk of period 3 were adequate time for the sheep to adapt to limited water availability. It is also possible that the sheep management, obvious health, and absence of heat stress during each of the 4 trials of this study allowed the sheep to activate various physiological mechanisms to cope with the 50% water restriction. Finally, the 3-way interactions in Fig.10 to 12 suggest that physiological responses to water restriction and speed of adaptation are not the same for sheep of each breed or region. For example, relatively low BW and DMI for KAT sheep from the MW suggests less resilience than for other sheep. In the final 2 wk of period 3, the sheep were expected to be fully adapted to restricting WI to 50% of ad libitum. However, the breed × region interaction for DMI in g/d showed that KAT sheep from the MW were lagging behind all the other sheep, indicating that they were less able to be fully adapted to that level of water restriction.

Changes During the Last Two Weeks of Period 3

The *P* values for average BW, DMI, WI, and the WI:DMI ratio during the last 2 wk of period 3 are shown in Table 9. There was a significant breed × region interaction for DMI in g/d (Table 10). This was primarily because of relatively low values for DOR sheep from the NW ($P \leq 0.212$) and KAT sheep from the MW ($P \leq 0.037$) and fairly similar values among regions for STC sheep. No significant region effects were detected for BW, DMI, or WI, but significant breed effects were found for DMI as a % of BW and in g/kg BW$^{0.75}$. In both cases, DMI was greater ($P < 0.05$) for STC than for DOR or KAT sheep which had similar ($P > 0.05$) values.

Spearman Ranking and Variance

Spearman rank correlation coefficients (*sr*) among periods and weeks and *P*-values for Bartlett's homogeneity of variance tests are displayed in Tables 11 and 12, respectively. In Table 11, the *sr* values among periods for DMI were significant for each breed and overall. The *sr* for DMI ranked period 1-2 > 2-3 > 1-3 for each breed and overall. However, *sr* values were greatest among breeds for STC and the difference in *sr* for periods 1-3 and 2-3 in STC was smaller than those for DOR or KAT. Comparisons among the 5 wk of period 3 when the sheep were offered water at 50% of ad libitum consumption are presented in Table 11. For DMI, all *sr* values among weeks were significant except for KAT sheep between wk 1 and wk 5 ($P = 0.120$). The *sr* for each breed also varied and were stronger between wk 1 and wk 2 ($sr \geq 0.88$) and weakest between wk 1 and wk 5 (i.e., 0.43, 0.24, and 0.73 for DOR, KAT, and STC sheep, respectively). The *sr* between wk 1 and wk ≥ 3 and between wk 2 and wk ≥ 3 were greater for STC than overall values and those for DOR and KAT.

The fact that all spearman rank correlation coefficients among periods were different from 0 suggests that the rankings observed in period 1 can accurately predict the ranking in periods 2 and 3 for DMI. In the context of treatments applied, the ranking in DMI of sheep of each breed in period 1 without water restriction is also consistent with the rankings during conditions of limited water availability in periods 2 and 3. The fact that STC sheep had the strongest prediction strength among periods for DMI may be related to how DMI for STC was least responsive to water restriction levels than other breeds in this study. Within period 3, it can be inferred that the rankings in DMI by DOR and STC sheep in wk 1 can reasonably predict the rankings in the 4 subsequent weeks. The reason why prediction accuracy could not be made for DMI by KAT sheep between wk 1 and 5 is unclear, but for most sheep in each breed, the rankings in wk 1 were less reflective of rankings in wk 5. Thus, rankings of sheep for DMI were less correlated when comparisons were made between time periods (weeks) that were farther apart from each other.

Homogeneity of variance for BW, DMI, and WI during the last 2 wk of period 3 is presented in Table 12. Variation in BW, DMI as a % of BW, and WI, regardless of how expressed, was similar ($P > 0.05$) among breeds. However, the variance was not homogenous among breeds for DMI in g/d ($P = 0.007$) and was smaller for STC than DOR or KAT sheep. Although not statistically significant ($P = 0.072$), the variance for DMI in g/kg $BW^{0.75}$ was numerically smaller for STC than other breeds. The variance for the WI:DMI ratio among breeds was also not homogenous ($P < 0.001$), with KAT sheep having larger variability than DOR and STC. In general, the homogeneity of variance tests for DMI in g/d and the WI:DMI ratio showed that restricting WI to 50% of ad libitum can have different effects on the 3 breeds evaluated. Although the lower variability in DMI by STC sheep is difficult to interpret in regard to resilience differences between breeds, it suggests that the majority of individual sheep had stabilized their DMI patterns near the end of the experiment. The larger WI:DMI variance for KAT sheep is also difficult to interpret considering that sample size was slightly larger for KAT than for DOR and STC sheep. However, KAT sheep did drink more water in g/d than other breeds and had a larger DMI variance than STC sheep on a g/d basis. Notably, all other response variables had approximately equal variance among breeds.

CONCLUSION

In this study, resilience of 3 hair sheep breeds from 4 climatic regions to limited water availability was examined at 50% of ad libitum WI for 5 wk following a baseline and intermediate water restriction period of 2 wk each in which the sheep were offered 100 and 75% of ad libitum WI, respectively. Across breeds and regions, all sheep increased their BW when switched to water restriction at 75% of ad libitum intake and suffered minor weight losses when initially switched to 50% restriction. Among breeds, most sheep gained weight during the 5 wk in which water was restricted to 50% of ad libitum intake, suggesting that the hair sheep breeds had high resilience to limited water availability in the absence of heat stress. The minor weight loss detected between the baseline and first 2 wk of the most severe water restriction period displayed the sheep ability to cope with severe water deprivation, possibly by efficient use of the limited water available, decreasing DMI, and enhancing digestion and utilization of the feed nutrients.

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Table 1. Temperature, relative humidity (RH), heat load index (HLI), and temperature-humidity index (THI) (mean ± SEM) outside and inside the room where the hair sheep were housed during 4 trials[1]

Location[2]	Period	Time[3]	Temperature, ºC	RH, %	HLI	THI
Outside	1	Day	18.3 ± 7.31	56.9 ± 2.80	69.7 ± 11.32	43.3 ± 10.11
		Night	13.6 ± 6.71	74.5 ± 3.43	69.0 ± 11.54	45.4 ± 11.76
	2	Day	21.3 ± 6.00	51.5 ± 3.93	72.2 ± 9.73	44.6 ± 8.60
		Night	16.1 ± 5.78	70.3 ± 3.63	71.3 ± 9.77	47.0 ± 9.76
	3	Day	21.1 ± 4.32	54.6 ± 3.46	73.2 ± 7.85	46.3 ± 7.44
		Night	15.9 ± 4.17	73.6 ± 4.88	72.3 ± 8.18	48.5 ± 8.57
Inside	1	Day	23.4 ± 3.38	48.3 ± 5.05	74.3 ± 8.71	45.8 ± 10.82
		Night	22.9 ± 3.29	49.6 ± 4.08	74.0 ± 8.40	45.9 ± 10.25
	2	Day	19.7 ± 5.64	58.3 ± 3.73	72.3 ± 10.08	46.3 ± 9.78
		Night	18.8 ± 6.45	59.7 ± 1.99	71.4 ± 10.28	45.4 ± 9.53
	3	Day	18.8 ± 4.10	60.8 ± 5.75	71.9 ± 8.51	46.4 ± 8.81
		Night	17.6 ± 4.77	61.8 ± 4.08	70.4 ± 8.61	45.1 ± 8.55

[1] The sheep were offered water ad libitum intake for 2 wk (period 1), 75% of ad libitum intake for 2 wk (period 2), and 50% of ad libitum intake for 5 wk (period 3).
[2]Outside data were averages for 4 trials and inside data were averages for 3 trials.
[3]Daytime was from 0700 h to 1900 h and nighttime was from 1900 h to 0700 h.

Table 2. Ingredient and nutrient composition of diet fed to hair sheep

Item	Concentration
Ingredient, % as fed basis	
Cottonseed hulls	29.06
Ground corn	19.98
Dehydrated alfalfa	19.98
Wheat middlings	13.00
Cottonseed meal	8.99
Pelleting agent	4.99
Salt	1.00
Calcium carbonate	0.95
Ammonium chloride	1.00
Yeast	1.00
Vitamin-mineral mix[1]	0.05
Rumensin 90 premix[2]	0.01
Nutrient composition, dry matter basis[3]	
Ash, %	8.7 ± 0.43
Crude protein, %	18.6 ± 0.46
Neutral detergent fiber, %	37.7 ± 0.95
Gross energy, MJ/kg	16.9 ± 0.12

[1]Composition: 1.28% Zn; 0.96% Fe; 0.704% Mn; 0.16% Cu; 0.048% I; 0.032% Co; 26,460,000 IU/kg vitamin A; 6,615,000 IU/kg vitamin D_3, and 11,025 IU/kg vitamin E.
[2]Supplied 20% monensin.
[3]Analysis of weekly composite samples formed from daily samples.

Table 3. *P* values for effects of breed (B), region (R), animal set, and initial age on body weight (BW), dry matter intake (DMI), and water intake (WI) of hair sheep offered water ad libitum for 2 wk (period 1)

	Variable							
Source of variation[1]	BW, kg	DMI, g/d	DMI, % BW	DMI, g/kg $BW^{0.75}$	WI, g/d	WI, % BW	WI, g/kg $BW^{0.75}$	WI:DMI
B	<0.001	<0.001	0.009	0.751	<0.001	0.070	0.290	0.447
R	0.016	0.458	0.175	0.737	0.161	0.329	0.336	0.455
B*R	0.279	0.419	0.293	0.436	0.346	0.555	0.561	0.629
Set	<0.001	<0.001	0.201	0.158	<0.001	0.011	0.033	0.016
Age	0.269	0.798	0.406	0.597	0.141	0.043	0.047	0.053

[1]In each of 4 separate trials (9 wk each), a different set of sheep of 3 breeds (Dorper, Katahdin, and St. Croix) with each representing 4 U.S. climatic regions (the Midwest, Northwest, Southeast, and Central Texas) was used.

Table 4. Effects of breed and region on body weight (BW), dry matter intake (DMI), and water intake (WI) of hair sheep offered water ad libitum for 2 wk (period 1)

	Breed[1]				Region[2]				
Variable	DOR	KAT	STC	SEM	MW	NW	SE	TX	SEM
BW, kg	60.6[a]	62.2[a]	46.5[b]	1.32	57.6[ab]	60.0[a]	53.9[b]	54.3[b]	1.53
DMI, g/d	1308[a]	1302[a]	1049[b]	32.7	1231	1266	1192	1191	38.0
DMI, % BW	2.17	2.12	2.30	0.040	2.14	2.16	2.27	2.22	0.047
DMI, g/kg $BW^{0.75}$	60.2	59.2	59.4	1.07	58.7	59.2	60.6	59.9	1.24
WI, g/d	3598[b]	3935[a]	3112[c]	122.2	3512	3703	3304	3675	142
WI, % BW	6.11	6.59	6.99	0.267	6.30	6.39	6.50	7.06	0.311
WI, g/kg $BW^{0.75}$	168.4	182.3	179.2	6.58	171.2	174.9	171.7	188.7	7.65
WI:DMI	2.89	3.10	3.03	0.122	3.05	2.99	2.84	3.15	0.142

[1] DOR = Dorper; KAT = Katahdin; STC = St. Croix.

[2] MW = Midwest; NW = Northwest; SE = Southeast; TX = Central Texas.

[a,b,c]Main effect means without a common superscript letter differ ($P < 0.05$).

Table 5. *P* values for effects of breed (B), region (R), period (P), week within period (W), animal set, and initial age on body weight (BW), dry matter intake (DMI), and water intake (WI) of hair sheep[1]

	Variable							
Source of variation[2]	BW, kg	DMI, g/d	DMI, % BW	DMI, g/kg BW$^{0.75}$	WI, g/d	WI, % BW	WI, g/kg BW$^{0.75}$	WI:DMI
B	<0.001	<0.001	0.016	0.665	<0.001	0.062	0.294	0.203
R	0.026	0.447	0.314	0.822	0.150	0.391	0.367	0.315
P	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
W	<0.001	0.925	0.669	0.740	0.022	0.453	0.242	0.825
B*R	0.225	0.486	0.694	0.859	0.310	0.597	0.581	0.704
B*P	0.090	0.118	0.846	0.638	<0.001	0.001	0.055	0.650
B*W	0.751	0.820	0.722	0.743	0.496	0.760	0.683	0.644
R*P	0.020	0.064	0.115	0.099	0.002	0.022	0.101	0.421
R*W	0.347	0.768	0.863	0.844	0.985	0.959	0.973	0.967
P*W	<0.001	<0.001	0.001	0.001	0.231	0.537	0.525	0.011
B*R*P	0.373	0.053	0.123	0.086	0.266	0.002	0.026	0.014
B*R*W	0.799	0.998	0.997	0.997	0.993	0.972	0.978	0.915
B*P*W	0.076	0.731	0.932	0.894	0.768	0.936	0.902	0.821
R*P*W	0.644	0.966	0.939	0.955	0.999	0.986	0.993	0.977
B*R*P*W	0.823	0.992	0.994	0.994	0.997	0.988	0.991	0.977
Set	<0.001	<0.001	<0.001	0.003	<0.001	0.017	0.033	<0.001
Age	0.360	0.974	0.184	0.286	0.135	0.044	0.045	0.085

[1] The sheep were offered water ad libitum for 2 wk in period 1, 75% of ad libitum intake for 2 wk in period 2, and 50% of ad libitum intake for 2 wk of period 3.
[2] In each of 4 separate trials (9 wk each), a different set of sheep of 3 breeds (Dorper, Katahdin, and St. Croix) with each representing 4 U.S. climatic regions (the Midwest, Northwest, Southeast, and Central Texas) was used.

Table 6. Effects of breed and period on body weight (BW), dry matter intake (DMI), and water intake (WI) of hair sheep

		Breed[1]				Period[2]			
Variable	Breed	DOR	KAT	STC	SEM	1	2	3	SEM
BW, kg		61.0[a]	62.5[a]	46.7[b]	1.32				
DMI, g/d		1,242[a]	1,229[a]	989[b]	29.7				
DMI, % BW		2.06[b]	2.01[b]	2.18[a]	0.041				
DMI, g/kg $BW^{0.75}$		57.2	56.0	56.2	1.05				
WI, g/d	DOR					3,587[b]	2,657[d]	1,809[fg]	94.7
	KAT					3,925[a]	2,891[cd]	1,968[f]	
	STC					3,116[c]	2,312[e]	1,561[g]	
WI, % BW	DOR					6.09[b]	4.42[d]	3.04[e]	0.204
	KAT					6.56[ab]	4.75[cd]	3.28[e]	
	STC					7.06[a]	5.08[c]	3.42[e]	
WI, g/kg $BW^{0.75}$		124.8	134.8	133.2	4.88				
WI:DMI		2.23	2.40	2.38	0.076				

[1] DOR = Dorper; KAT = Katahdin; STC = St. Croix.

[2] The sheep were offered water ad libitum intake for 2 wk in period 1, 75% of ad libitum intake for 2 wk in period 2, and 50% of ad libitum for 2 wk of period 3.

[a,b]Mean effect means within a row without a common superscript letter differ ($P < 0.05$); presence of interaction means denotes a significant interaction ($P < 0.05$); [a,b,c,d,e,f,g]Interaction means without a common superscript letter differ ($P < 0.05$).

Table 7. *P* values for effects of breed (B), region (R), week (W), animal set, and initial age on body weight (BW), average daily gain (ADG), dry matter intake (DMI), and water intake (WI) of hair sheep offered water at 50% of ad libitum intake for 5 wk (period 3)

	Variable								
Source of variation[1]	BW, kg	ADG, g/d	DMI, g/d	DMI, % BW	DMI, g/kg $BW^{0.75}$	WI, g/d	WI, % BW	WI, g/kg $BW^{0.75}$	WI:DMI
B	0.399	0.714	0.198	0.148	0.539	0.963	0.947	0.930	0.281
R	0.138	0.165	0.808	0.421	0.418	0.367	0.017	0.026	0.406
W	<0.001	<0.001	<0.001	<0.001	<0.001	0.777	<0.001	<0.001	0.006
B*R	0.091	0.406	0.341	0.708	0.671	0.637	0.316	0.410	0.247
B*W	0.445	0.160	0.416	0.626	0.514	0.518	0.001	0.003	0.176
R*W	0.066	0.122	0.007	0.059	0.033	0.708	0.024	0.035	0.044
B*R*W	0.008	0.492	0.001	0.013	0.006	0.230	0.051	0.081	0.004
Set	0.351	0.002	0.009	<0.001	<0.001	0.002	0.045	0.006	0.004
Age	0.003	0.116	0.065	0.028	0.024	0.408	0.284	0.388	0.238
Covariate	<0.001	0.646	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

[1]In each of 4 separate trials (9 wk each), a different set of sheep of 3 breeds (Dorper, Katahdin, and St. Croix) with each representing 4 U.S. climatic regions (the Midwest, Northwest, Southeast, and Central Texas) was used.

Table 8. Effects of breed and week on body weight (BW), average daily gain (ADG), dry matter intake (DMI), and water intake (WI) of hair sheep offered water at 50% of ad libitum intake for 5 wk (period 3)

	Breed[1]				Week					
Variable	DOR	KAT	STC	SEM	1	2	3	4	5	SEM
BW, kg	56.9	56.9	56.3	0.28						
ADG, g/d	37	44	53	14.3	-109^{d}	35^{c}	83^{b}	64^{bc}	152^{a}	18.0
DMI, g/d	1,075	1,055	1,002	26.2						
DMI, % BW	1.89	1.86	1.97	0.041						
DMI, g/kg BW$^{0.75}$	51.7	50.6	52.3	1.08						
WI, g/d	1,749	1,747	1,750	7.4						
WI:DMI	1.70	1.84	1.73	0.064						

[1] DOR = Dorper; KAT = Katahdin; STC = St. Croix.

[a,b,c,d] Mean effect means within a row without a common superscript letter differ ($P < 0.05$).

Table 9. *P* values for effects of breed (B), region (R), animal set, and initial age on body weight (BW), dry matter intake (DMI), and water intake (WI) of hair sheep offered water at 50% of ad libitum intake during the last 2 wk of period 3

	Variable							
Source of variation[1]	BW, kg	DMI, g/d	DMI, % BW	DMI, g/kg $BW^{0.75}$	WI, g/d	WI, % BW	WI, g/kg $BW^{0.75}$	WI:DMI
B	0.817	0.637	0.013	0.045	0.840	0.457	0.327	0.076
R	0.612	0.493	0.303	0.145	0.457	0.648	0.642	0.290
B*R	0.783	0.029	0.408	0.053	0.758	0.841	0.711	0.061
Set	0.021	<0.001	<0.001	<0.001	0.001	0.004	0.001	<0.001
Age	0.005	0.075	0.030	0.027	0.397	0.390	0.457	0.364
Covariate	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

[1]In each of 4 separate trials (9 wk each), a different set of sheep of 3 breeds (Dorper, Katahdin, and St. Croix) with each representing 4 U.S. climatic regions (the Midwest, Northwest, Southeast, and Central Texas) was used.

Table 10. Effects of breed and region on body weight (BW), dry matter intake (DMI), and water intake (WI) of hair sheep offered water at 50% of ad libitum intake during the last 2 weeks of period 3

		Breed[1]				Region[2]				
Variable	Breed	DOR	KAT	STC	SEM	MW	NW	SE	TX	SEM
BW, kg		57.5	57.4	57.0	0.56	57.0	56.9	57.4	57.9	0.62
DMI, g/d		1,071	1,051	1,032	28.6					
	DOR					1,143[a]	980[bc]	1,078[ab]	1,083[ab]	57.4
	KAT					904[c]	1,058[ab]	1,126[ab]	1,114[ab]	
	STC					1,068[ab]	1,017[abc]	999[abc]	1,043[abc]	
DMI, % BW		1.87[b]	1.81[b]	2.01[a]	0.049	1.85	1.83	1.96	1.94	0.056
DMI, g/kg $BW^{0.75}$		51.1[ab]	49.7[b]	53.5[a]	1.04	50.3	49.8	53.1	52.6	1.25
WI, g/d		1,751	1,750	1,742	11.1	1,752	1,752	1,731	1,757	12.8
WI, % BW		3.17	3.16	3.07	0.065	3.17	3.18	3.07	3.12	0.075
WI, g/kg $BW^{0.75}$		85.9	85.8	83.3	1.53	85.7	86.1	83.4	84.8	1.77
WI:DMI		1.71	1.90	1.64	0.082	1.81	1.87	1.64	1.68	0.098

[1] DOR = Dorper; KAT = Katahdin; STC = St. Croix.
[2] MW = Midwest; NW = Northwest; SE = Southeast; TX = Central Texas.
[a,b]Mean effect means within a row without a common superscript letter differ ($P < 0.05$); presence of interaction means denotes a significant interaction ($P < 0.05$); [a,b,c]Interaction means without a common superscript letter differ ($P < 0.05$).

Table 11. Spearman rank correlation coefficients (*sr*) between periods and between weeks in period 3 for dry matter intake in g/d for hair sheep[1]

		Breed[2]							
		DOR		KAT		STC		Overall	
Variable		*sr*	*P*	*sr*	*P*	*sr*	*P*	*sr*	*P*
Periods	1 and 2	0.79	<0.001	0.81	<0.001	0.88	<0.001	0.85	<0.001
	1 and 3	0.31	0.003	0.30	0.005	0.60	<0.001	0.51	<0.001
	2 and 3	0.60	<0.001	0.55	<0.001	0.67	<0.001	0.67	<0.001
Weeks	1 and 2	0.88	<0.001	0.89	<0.001	0.90	<0.001	0.91	<0.001
	1 and 3	0.72	<0.001	0.73	<0.001	0.90	<0.001	0.83	<0.001
	1 and 4	0.48	0.001	0.51	0.001	0.78	<0.001	0.60	<0.001
	1 and 5	0.43	0.004	0.24	0.120	0.73	<0.001	0.53	<0.001
	2 and 3	0.77	<0.001	0.68	<0.001	0.94	<0.001	0.85	<0.001
	2 and 4	0.56	<0.001	0.54	<0.001	0.78	<0.001	0.65	<0.001
	2 and 5	0.48	<0.001	0.31	0.049	0.66	<0.001	0.53	<0.001
	3 and 4	0.84	<0.001	0.87	<0.001	0.86	<0.001	0.85	<0.001
	3 and 5	0.76	<0.001	0.65	<0.001	0.72	<0.001	0.74	<0.001
	4 and 5	0.85	<0.001	0.82	<0.001	0.84	<0.001	0.86	<0.001

[1]The sheep were offered water ad libitum intake in period 1, 75% of ad libitum intake in period 2, and 50% of ad libitum intake in period 3.
[2]DOR = Dorper; KAT = Katahdin; STC = St. Croix.

Table 12. Homogeneity of variance in body weight (BW), dry matter intake (DMI), and water intake (WI) during the last 2 wk of offering water at 50% of ad libitum intake to hair sheep[1]

		SD[2]		
Variable	*P*[3]	DOR	KAT	STC
BW, kg	0.982			
DMI, g/d	0.007	241.2	232.8	152.0
DMI, % BW	0.719			
DMI, g/kg$^{0.75}$	0.072	9.98	11.04	7.76
WI, g/d	0.881			
WI, % BW	0.656			
WI, g/kg$^{0.75}$	0.573			
WI:DMI	<0.001	0.49	0.94	0.44

[1]DOR = Dorper; KAT = Katahdin; STC = St. Croix.
[2]SD = standard deviation (shown for $P \leq 0.072$).
[3]*P* value for the Bartlett test.

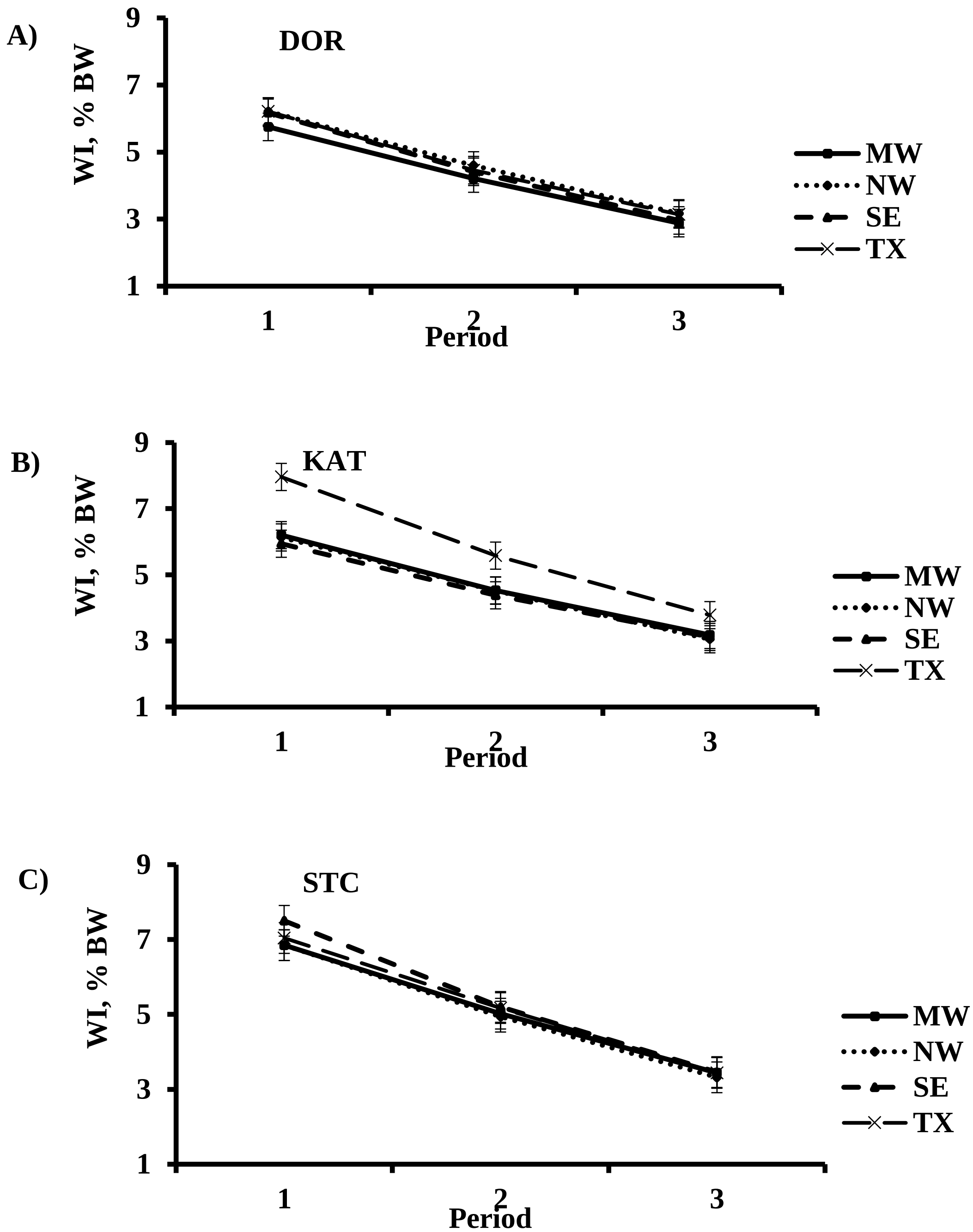

Figure 1. Water intake (WI) in % BW of Dorper (DOR), Katahdin (KAT), and St. Croix (STC) sheep from the Midwest (MW), Northwest (NW), Southeast (SE), and Central Texas (TX) when offered water ad libitum in period 1, at 75% of ad libitum intake in period 2, and at 50% of ad libitum intake in period 3.

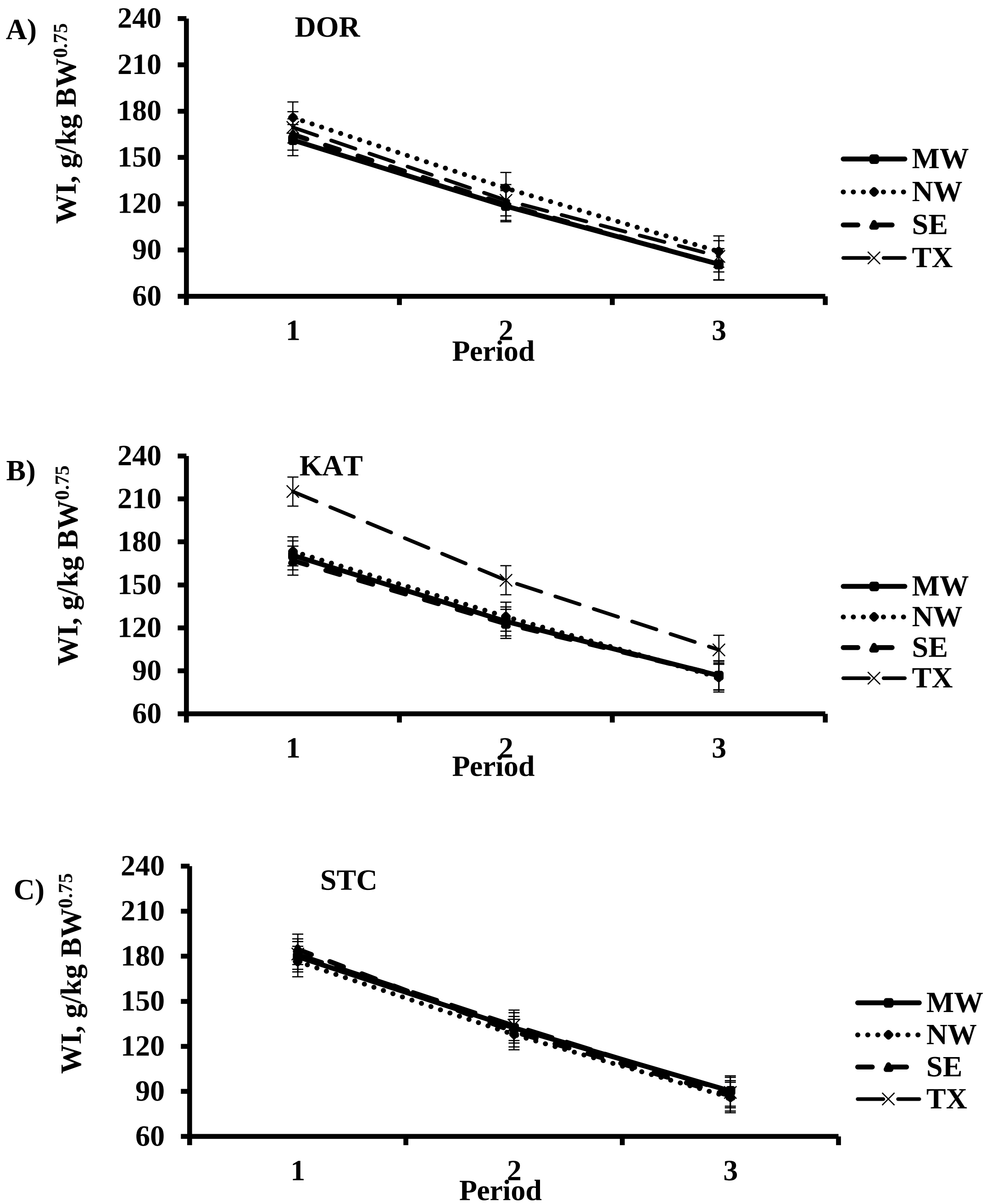

Figure 2. Water intake (WI) in g/kg BW$^{0.75}$ of Dorper (DOR), Katahdin (KAT), and St. Croix (STC) sheep from the Midwest (MW), Northwest (NW), Southeast (SE), and Central Texas (TX) when offered water ad libitum in period 1, at 75% of ad libitum intake in period 2, and at 50% of ad libitum intake in period 3.

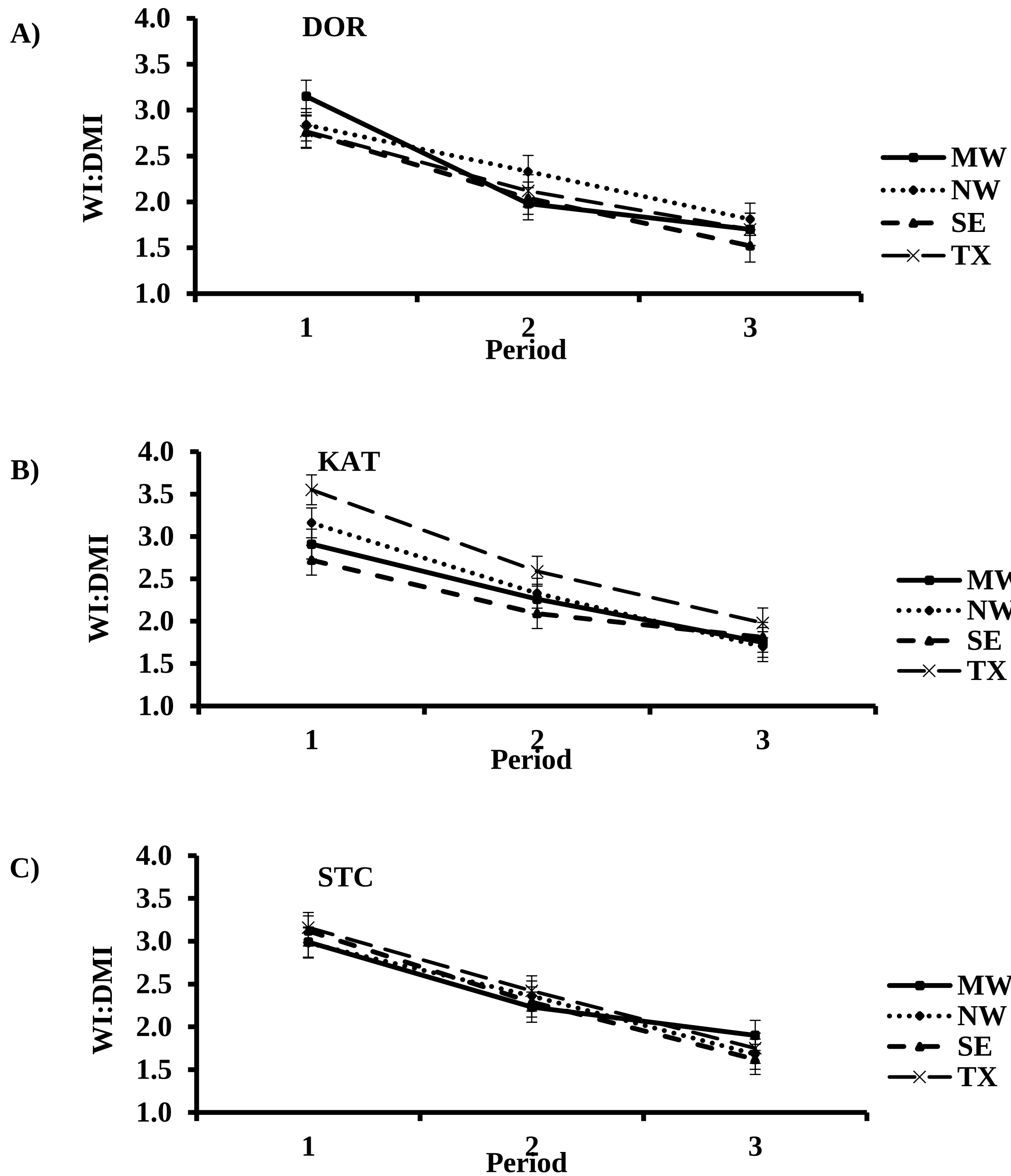

Figure 3. Water intake (WI) relative to dry matter intake (DMI) of Dorper (DOR), Katahdin (KAT), and St. Croix (STC) sheep from the Midwest (MW), Northwest (NW), Southeast (SE), and Central Texas (TX) when offered water ad libitum in period 1, at 75% of ad libitum intake in period 2, and at 50% of ad libitum intake in period 3.

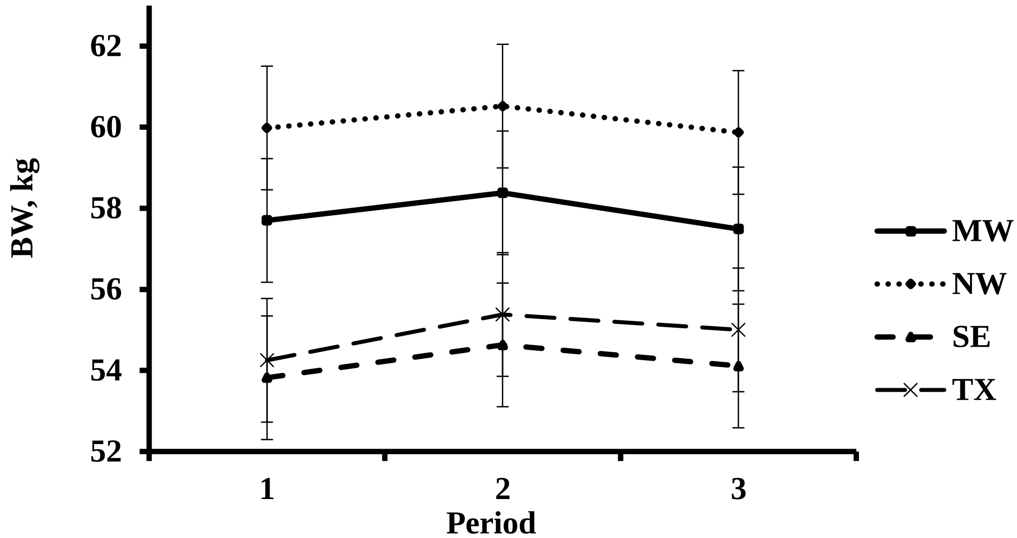

Figure 4. Body weight (BW) of hair sheep from the Midwest (MW), Northwest (NW), Southeast (SE), and Central Texas (TX) when offered water ad libitum (period 1), at 75% of ad libitum intake (period 2), and at 50% of ad libitum intake (period 3).

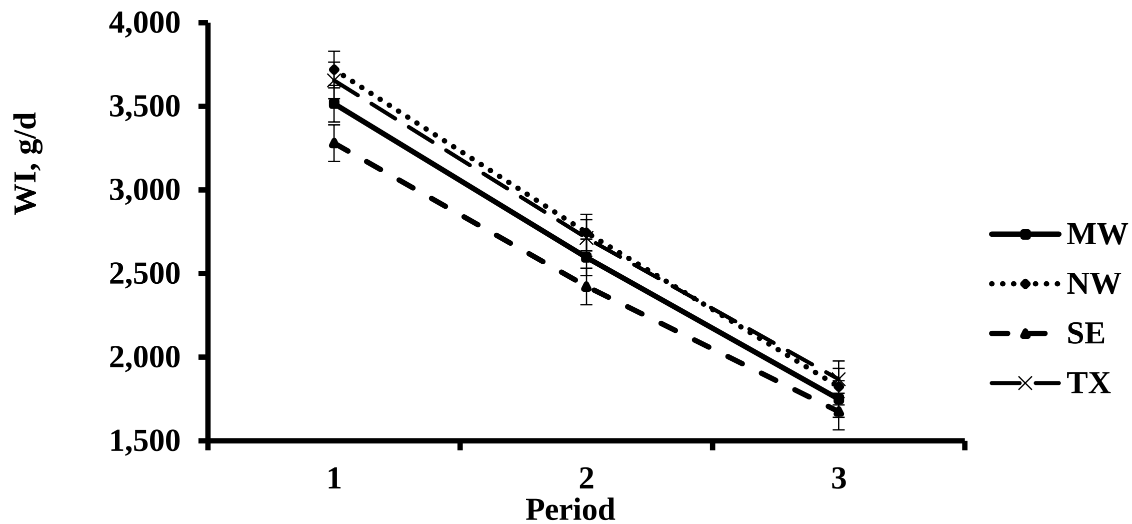

Figure 5. Water intake (WI) of hair sheep from the Midwest (MW), Northwest (NW), Southeast (SE), and Central Texas (TX) when offered water ad libitum in period 1, at 75% of ad libitum intake in period 2, and at 50% of ad libitum intake in period 3.

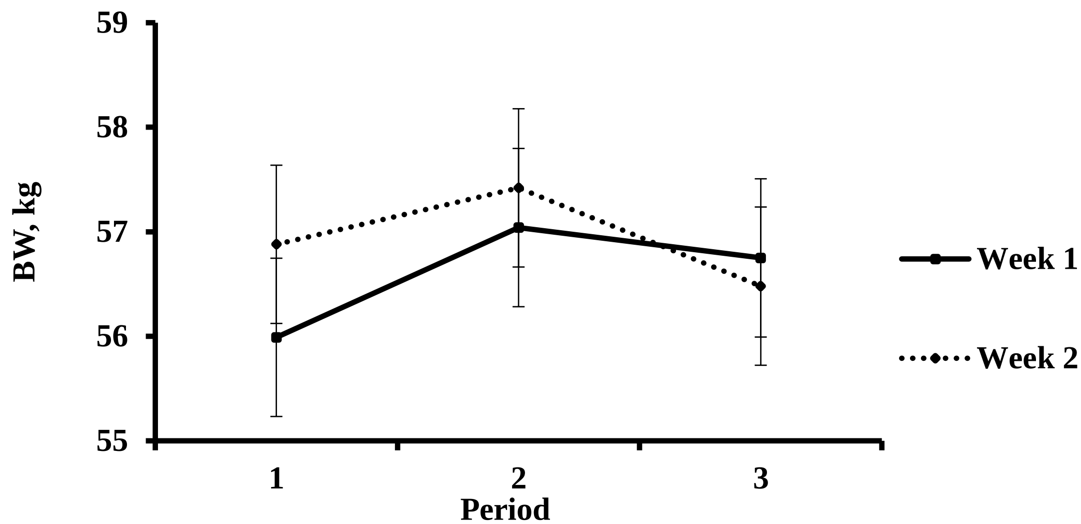

Figure 6. Differences between week within period in body weight (BW) of hair sheep offered water ad libitum in period 1, at 75% of ad libitum intake in period 2, and at 50% of ad libitum intake in period 3.

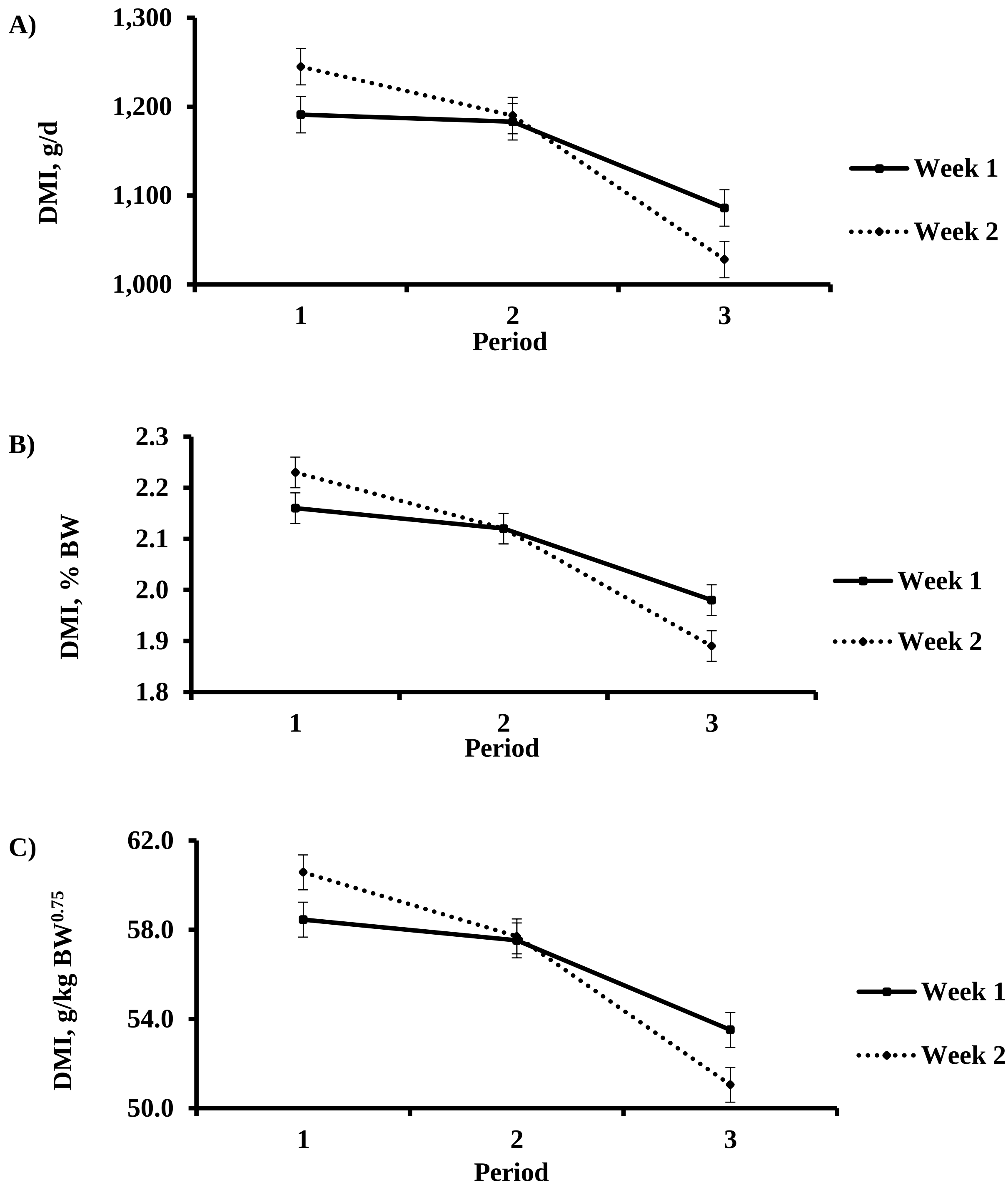

Figure 7. Differences between week within period in dry matter intake (DMI) of hair sheep offered water ad libitum in period 1, at 75% of ad libitum intake in period 2, and at 50% of ad libitum intake in period 3.

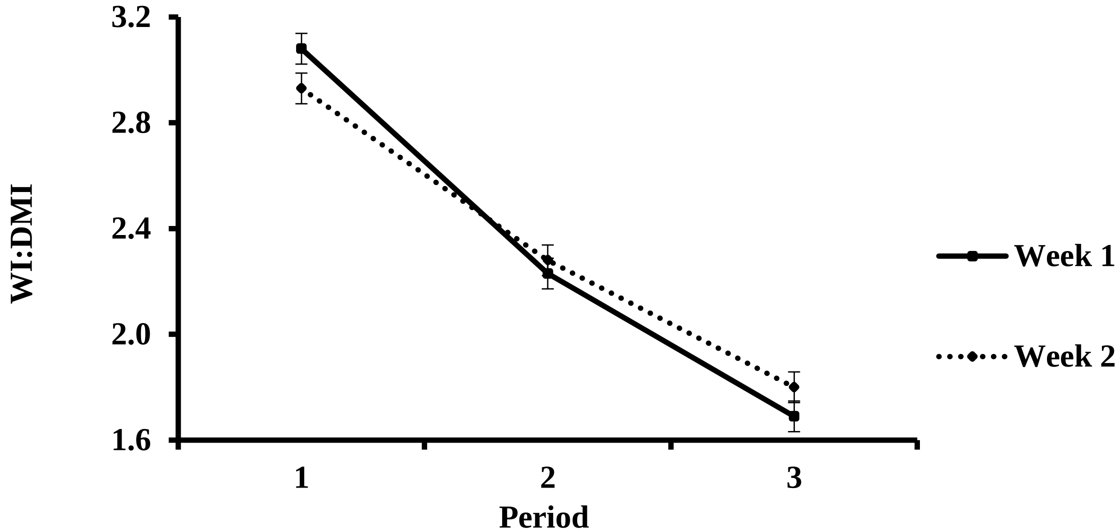

Figure 8. Differences between week within period in water intake (WI) relative to dry matter intake (DMI) of hair sheep offered water ad libitum in period 1, at 75% of ad libitum intake in period 2, and at 50% of ad libitum intake in period 3.

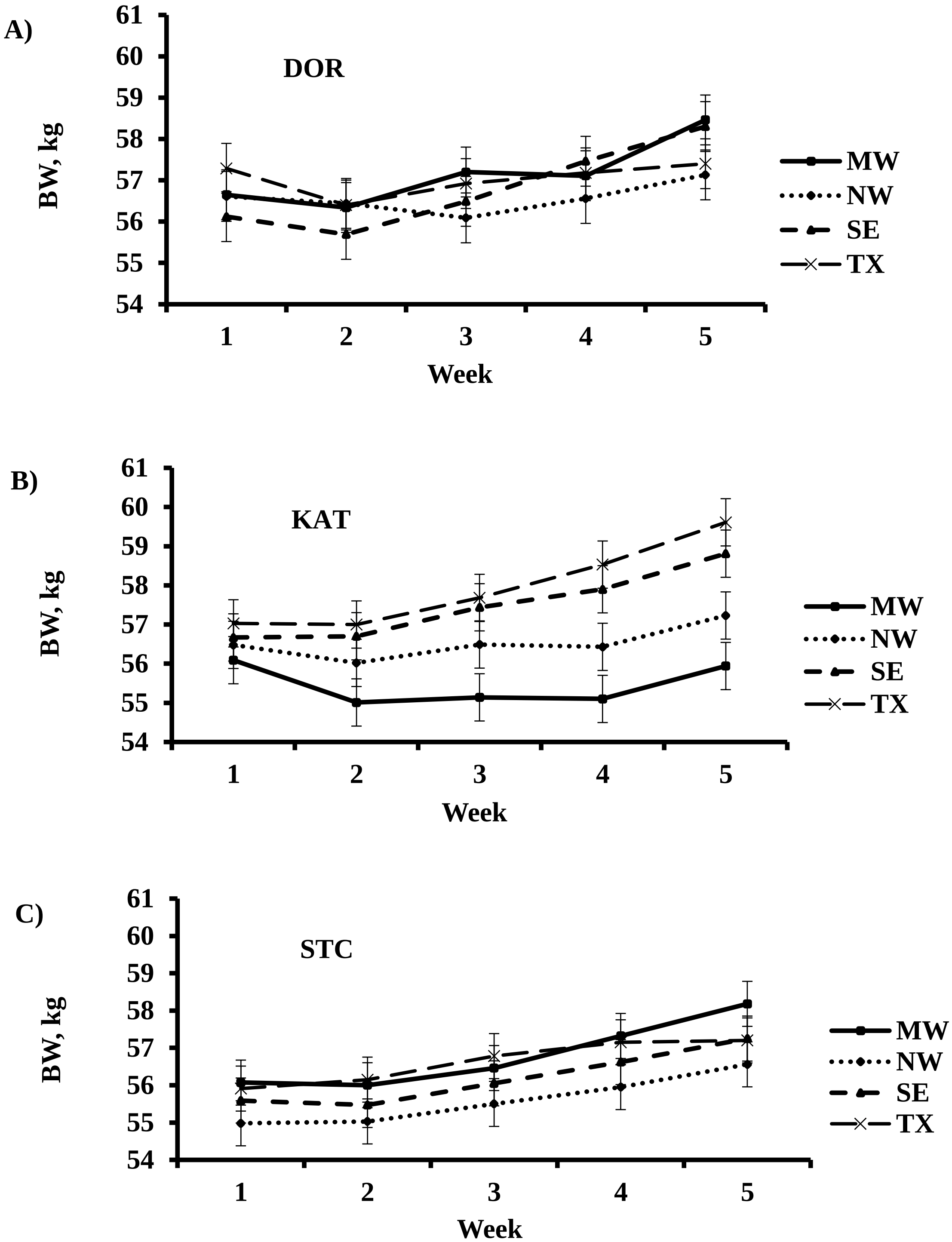

Figure 9. Weekly body weight (BW) of Dorper (DOR), Katahdin (KAT), and St. Croix (STC) sheep from the Midwest (MW), Northwest (NW), Southeast (SE), and Central Texas (TX) when offered water at 50% of ad libitum intake in period 3.

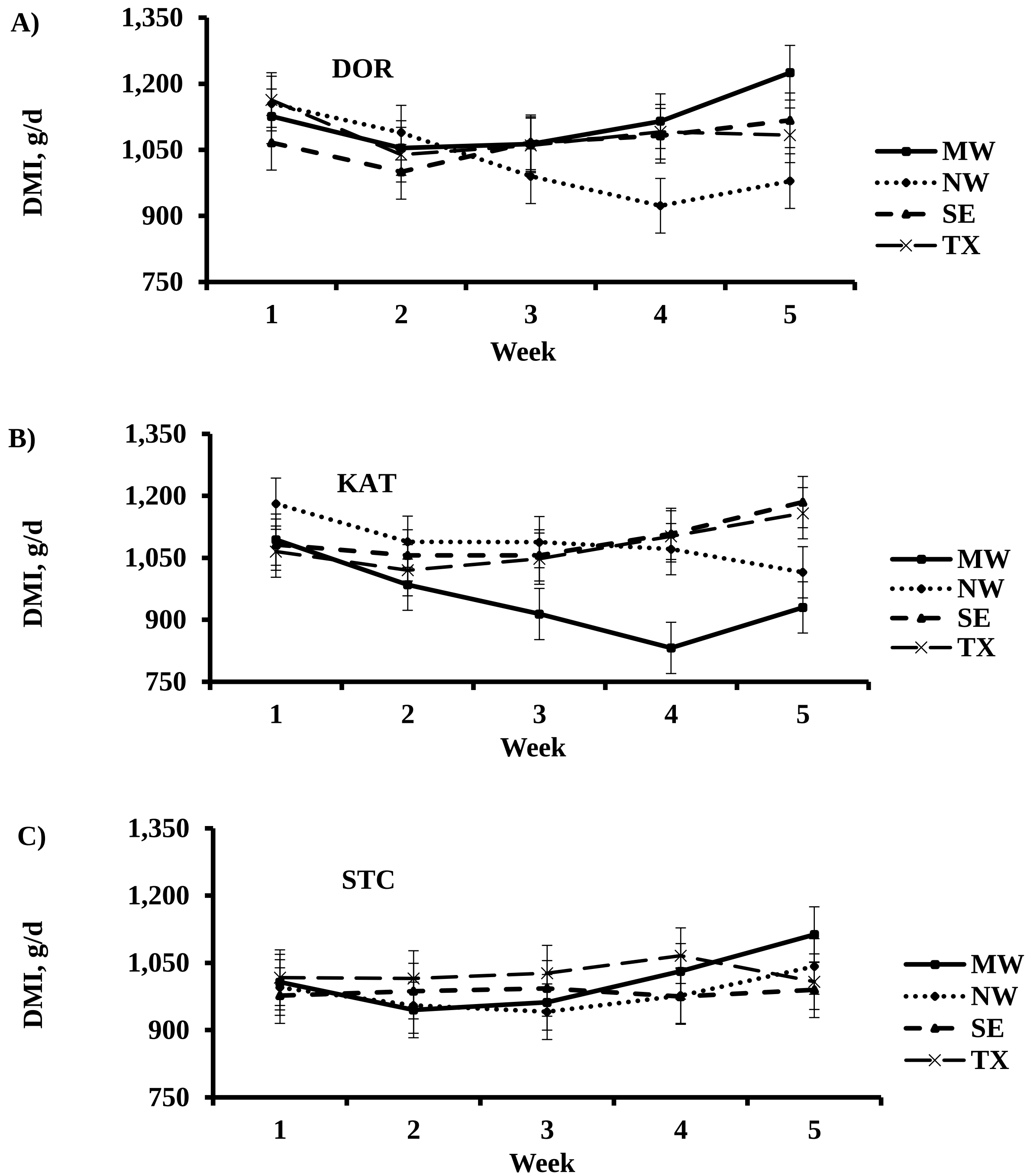

Figure 10. Weekly dry matter intake (DMI) in g/d of Dorper (DOR), Katahdin (KAT), and St. Croix (STC) sheep from the Midwest (MW), Northwest (NW), Southeast (SE), and Central Texas (TX) when offered water at 50% of ad libitum intake in period 3.

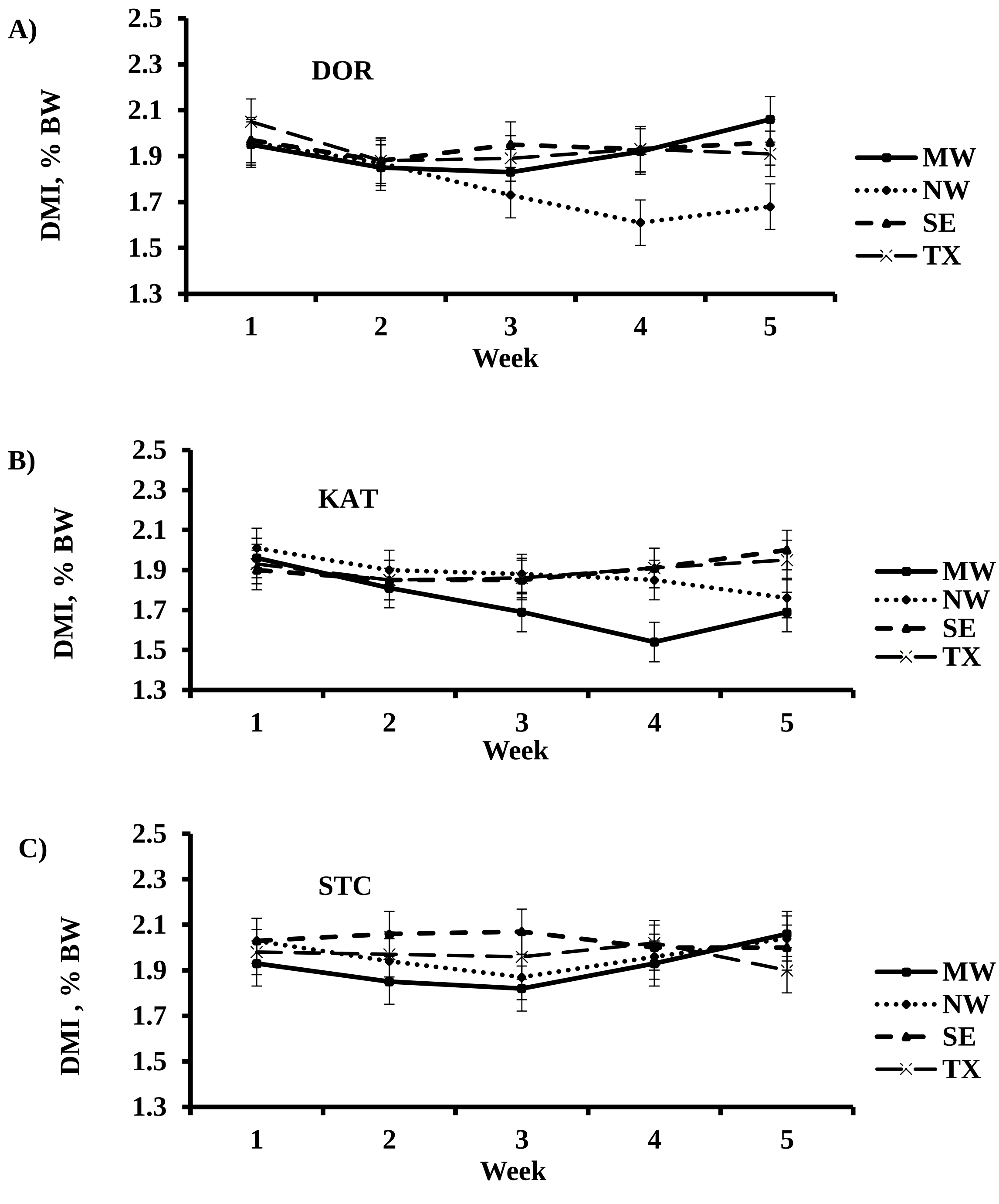

Figure 11. Weekly dry matter intake (DMI) as % of body weight (BW) of Dorper (DOR), Katahdin (KAT), and St. Croix (STC) sheep from the Midwest (MW), Northwest (NW), Southeast (SE), and Central Texas (TX) when offered water at 50% of ad libitum intake in period 3.

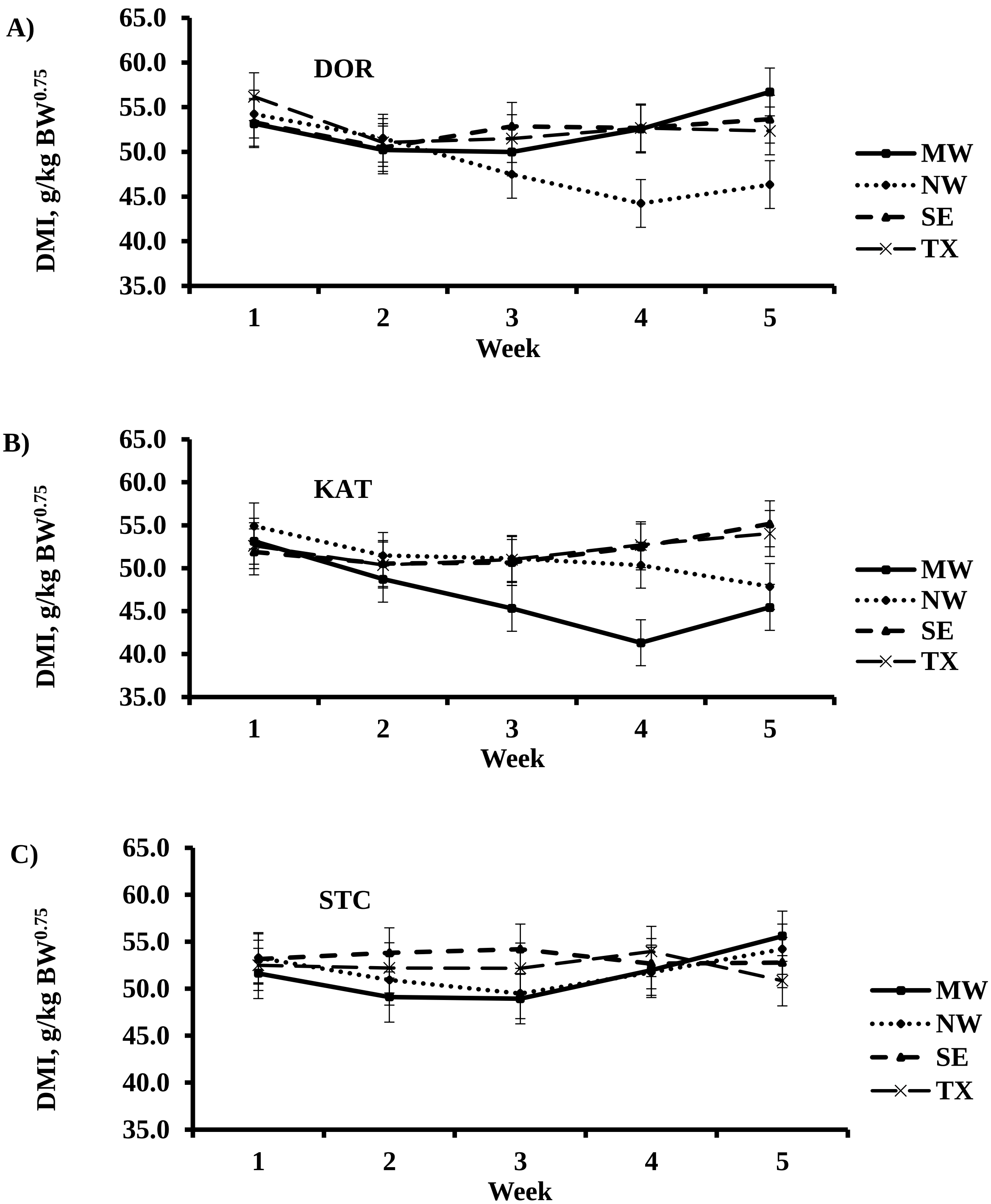

Figure 12. Weekly dry matter intake (DMI) in g/kg of metabolic body weight (BW) of Dorper (DOR), Katahdin (KAT), and St. Croix (STC) sheep from the Midwest (MW), Northwest (NW), Southeast (SE), and Central Texas (TX) when offered water at 50% of ad libitum intake in period 3.

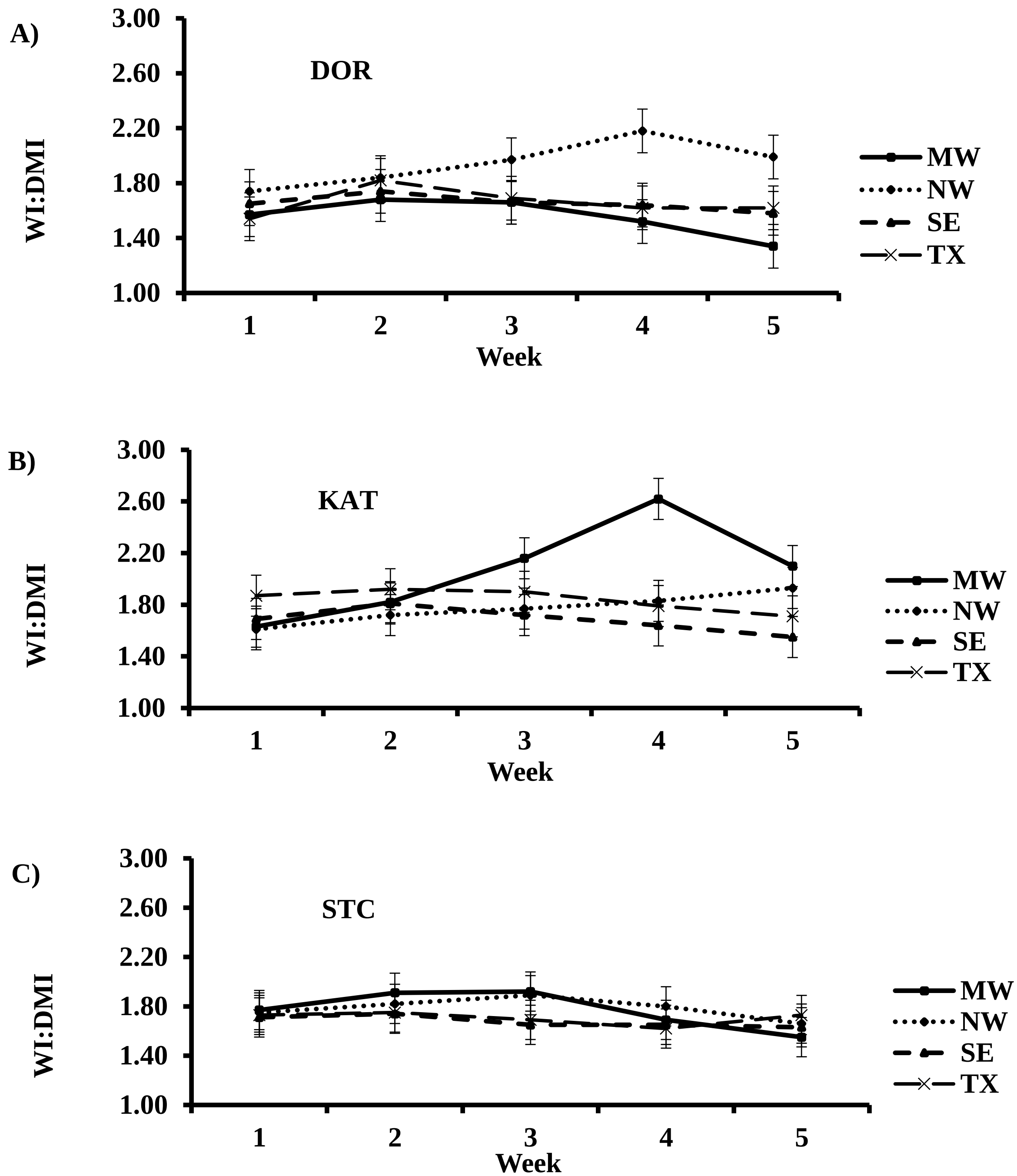

Figure 13. Weekly water intake (WI) relative to dry matter intake (DMI) of Dorper (DOR), Katahdin (KAT), and St. Croix (STC) sheep from the Midwest (MW), Northwest (NW), Southeast (SE), and Central Texas (TX) when offered water at 50% of ad libitum intake in period 3.

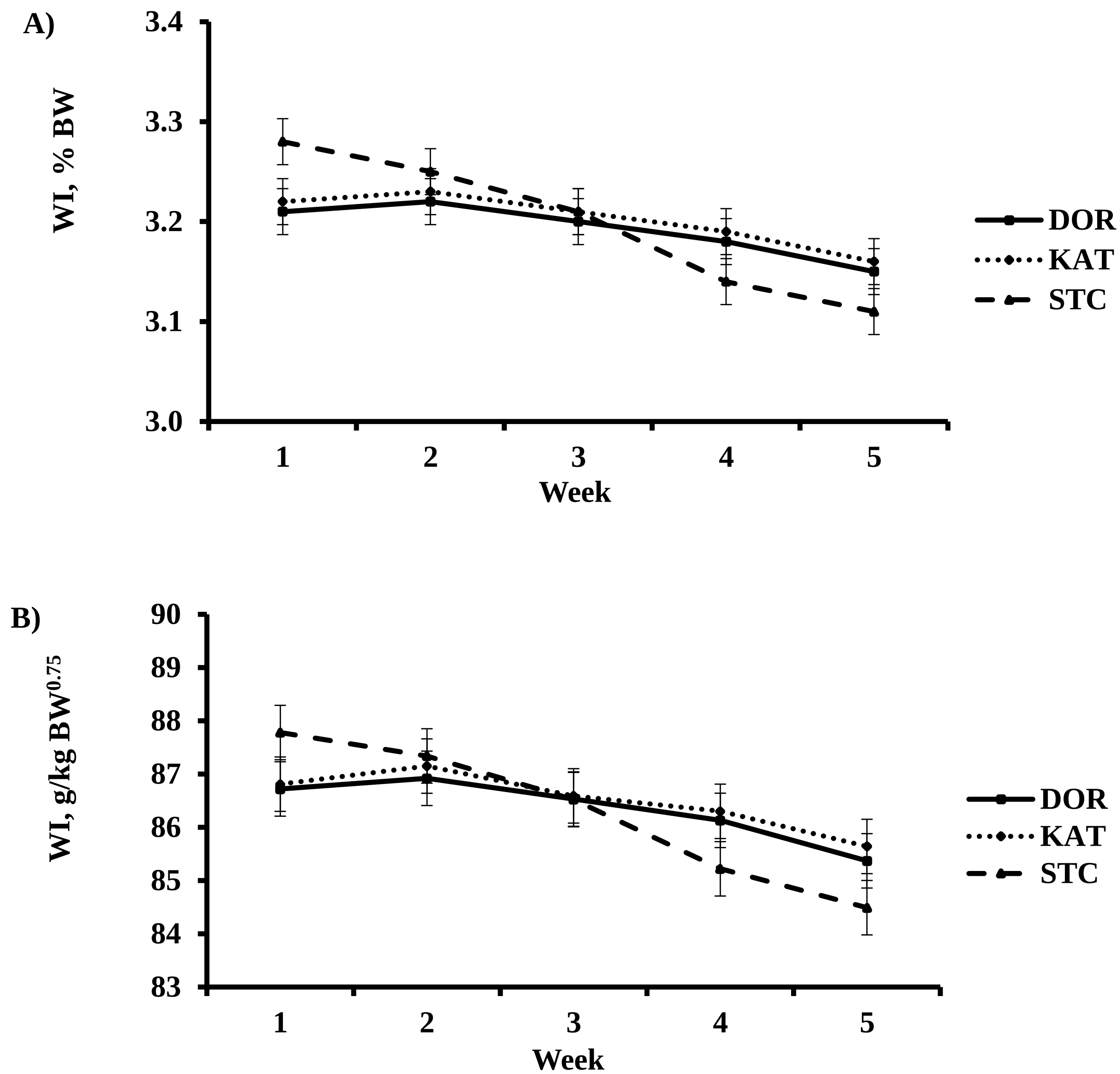

Figure 14. Weekly water intake (WI) of Dorper (DOR), Katahdin (KAT), and St. Croix (STC) sheep offered water at 50% of ad libitum intake in period 3.

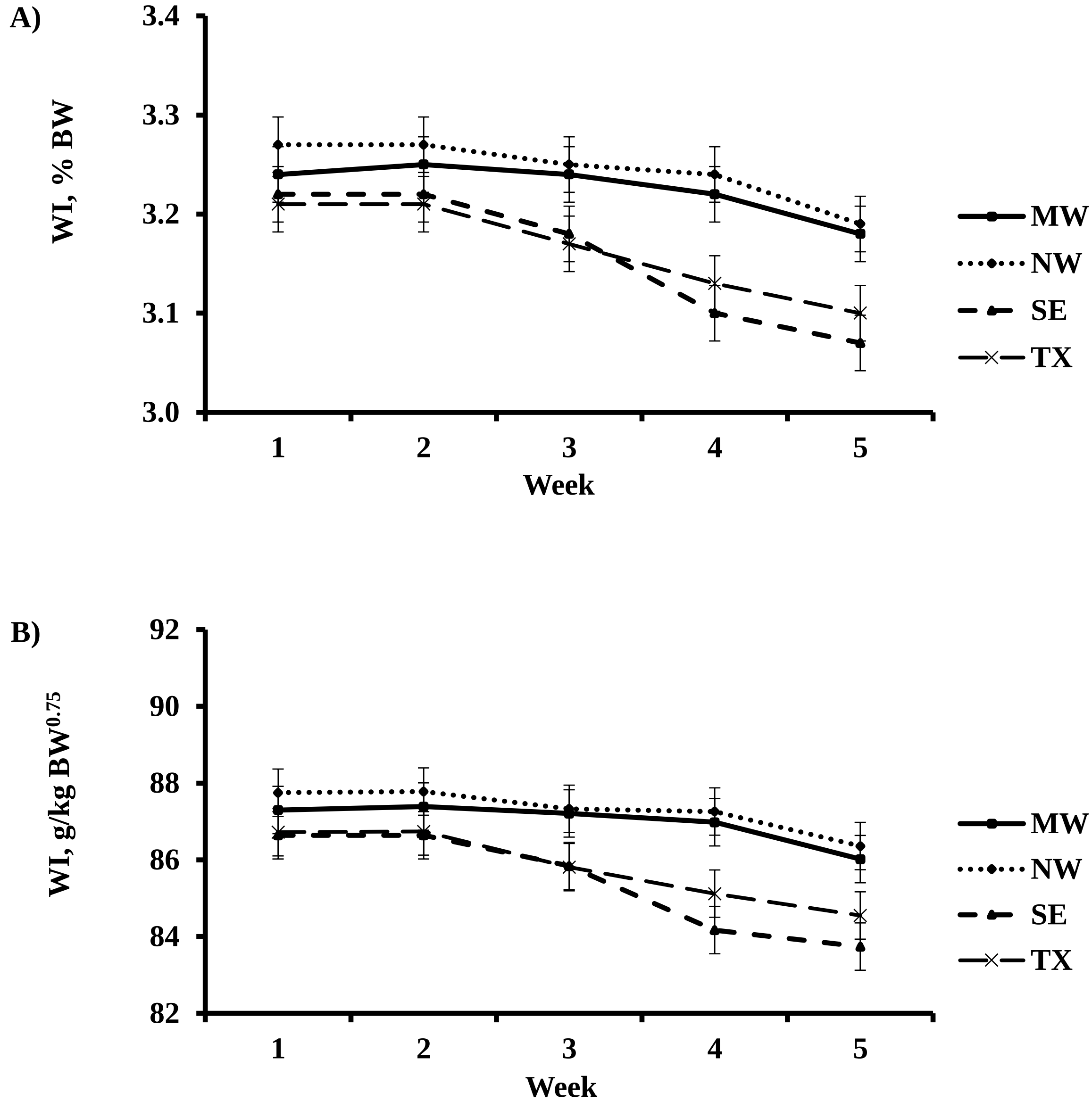

Figure 15. Weekly water intake (WI) of hair sheep from the Midwest (MW), Northwest (NW), Southeast (SE), and Central Texas (TX) when offered water at 50% of ad libitum intake in period 3.

CHAPTER IV

EFFECTS OF RESTRICTED AVAILABILITY OF DRINKING WATER ON PHYSIOLOGICAL RESPONSES IN HAIR SHEEP BREEDS FROM DIFFERENT REGIONS OF THE UNITED STATES

ABSTRACT

Physiological responses of hair sheep breeds from different U.S. regions to water restriction were evaluated using 43 Dorper (DOR), 43 Katahdin (KAT), and 44 St. Croix (STC) female sheep with initial body weight (BW) of 60 ± 2.6, 63 ± 2.4, and 45 ± 2.1 kg, respectively, and age of 3.5 ± 0.19 yr. The sheep were derived from the Midwest (MW) Northwest (NW), Southeast (SE), and central Texas (TX) with all breeds represented within each of the 4 climatic regions. In 4 separate trials using different sets of sheep in the spring and summer of 2016 and 2017, the sheep were housed individually and fed a pelleted diet at 160% of the metabolizable energy requirement for maintenance. In each trial, all sheep were offered water ad libitum for 2 wk (period 1), 75% of ad libitum intake for 2 wk (period 2), and 50% of ad libitum intake for 5 wk (period 3) at 0730 h. Blood samples were collected once at 0800 and once at 1400 h each week for measurement of characteristics and components sensitive to water shortage. Data from the 4 trials were pooled and analyzed for effects of and interactions involving breed, region, period, week within period, and time of blood sampling. A breed × period

interaction ($P < 0.05$) showed the lowest ($P < 0.05$) plasma osmolality for DOR (300 mosm/L) in period 1 and the highest ($P < 0.05$) for both KAT and STC (309 mosm/L) in period 3. It also showed the lowest ($P < 0.05$) blood packed cell volume (PCV) for KAT (30.7%) in period 1 and the highest ($P < 0.05$) for STC (33.2%) in period 3. Despite the minor osmolality and PCV differences among breeds in period 1 (averaging 301.7 mosm/L and 31.5%), they increased ($P < 0.05$) to similar ($P > 0.05$) levels in period 3 (averaging 308.3 mosm/L and 32.4%). The sheep breed did not affect ($P > 0.05$) hemoglobin (Hb) concentration (averaging 12.12 g/dL), but STC had higher ($P < 0.05$) O_2 saturation (71.9 vs. 65.9%) and concentration (11.77 vs. 10.65 mmol/L) than DOR or KAT, which had similar ($P > 0.05$) values. Serum concentration of triglycerides was higher ($P < 0.05$) for KAT (34.8 g/dL) than for DOR or STC (averaging 29.1 g/dL; $P > 0.05$). Other serum metabolites were not affected ($P > 0.05$) by breed. Serum concentrations of albumin, cholesterol, creatinine, glucose, triglycerides, and urea, however, were affected by period, as they increased ($P < 0.05$) in period 3 by 3.5, 25.0, 15.7, 7.6, 21.9, and 15.5% above baseline levels, respectively. In period 3, there was a breed × region × week interaction ($P < 0.05$) showing that while most sheep had similar PCV and Hb concentration each week, DOR from the NW had the lowest ($P < 0.05$) values. A region × week interaction ($P < 0.05$) also revealed that plasma osmolality in wk 1 (309 to 313 mosm/L) decreased ($P < 0.05$) in wk 2 (304 to 308 mosm/L) and did not change ($P > 0.05$) thereafter. In period 3, STC had higher ($P < 0.05$) concentrations of O_2 (12.32 vs. 11.17 mmol/L) and glucose (60.1 vs. 55.6 mg/dL) and lower ($P < 0.05$) creatinine concentration (0.868 vs. 0.943 mg/dL) than DOR or KAT, which had similar ($P > 0.05$) concentrations. In the last 2 wk of period 3, STC had higher ($P < 0.05$) PCV

(33.6 vs. 31.7%) and concentrations of Hb (12.60 vs. 12.02 g/dL) and glucose (59.2 vs. 54.0 mg/dL), but lower ($P < 0.05$) creatinine concentration (0.838 vs. 0.917 mg/dL) than DOR or KAT. Based on the minor increases in some blood measurements or metabolites during water restriction at 50% of ad libitum intake in the absence of heat stress conditions, it is concluded that the 3 sheep breeds are highly resilient to limited drinking water availability.

Key words: blood characteristics, hair sheep, resilience, water restriction

INTRODUCTION

Climate change has affected and is expected to continue to threaten sustainable animal agriculture systems worldwide through rising temperatures, changing rainfall patterns, and expansion of droughts (Hatfield et al., 2008; Thornton et al., 2009; Misra, 2014). The direct and indirect impacts of climate change on ruminants include negative effects on production and reproduction as well as compromised metabolic functions, immune system, and overall health which result in major economic losses (Hatfield et al., 2008; Rust and Rust, 2013; Sejian, 2013). Because adaptation of small ruminants to climate change through endocrine, biochemical, and molecular responses have been demonstrated, recent efforts have been directed towards identification and characterization of sheep and goat breeds resistant to heat stress and drought (Sejian, 2013). However, for those efforts to result in breeding and management strategies to cope with climate change, a database of original research evaluating the impact of high environmental temperatures (Brown et al., 1988; Silanikove, 2000a; Seixas et al., 2017) and droughts (Khan et al., 1978; Igbokwe, 1993; Kaliber et al., 2016) on small ruminants must be established.

Due to the severe and more frequent droughts in arid and semiarid environments, studies have focused on adaptation of local breeds of sheep (Nejad et al., 2014; Kumar et al., 2016; Casamassima et al., 2017) and goats (Hossaini-Hilali et al., 1994; Ahmed and El Kheir, 2004; Alamer, 2009) to limited water availability by monitoring performance. To elucidate the physiological mechanisms by which adapted sheep or goats cope with drought, other studies have monitored certain blood characteristics and metabolites sensitive to drinking water shortage in sheep (Aganga et al., 1989; Hamadeh et al., 2006; De et al., 2015) and goat (Alamer, 2006; Mengistu et al., 2007a; Kaliber et al., 2016) breeds differing in resilience to water restriction. Hair sheep breeds are well adapted to the adverse climates of arid and tropical regions but have not been evaluated for their resilience to limited water availability even though they have been increasingly spreading worldwide, including in the U.S. Hair sheep have been shown to have higher fertility, prolificacy, survivability, and production of meat than many wool sheep raised under similar conditions (Bradford et al., 1983; Bunge et al., 1993; Wildeus, 1997). They also exhibit more resistance to gastrointestinal parasites (Burke and Miller, 2004) and are more efficient (Silva et al., 2004) than or similar (Quick and Dehority, 1986; Mann et al., 1987) to wool sheep in utilizing low or moderate quality forages. For these reasons and others, especially freedom from wool, it was concluded that hair sheep are more economically viable than wool sheep through reducing production costs and facilitating entry of new producers into the U.S. sheep industry (Wildeus, 1997; Notter, 2000).

As a consequence of the increasing importance of hair sheep to animal agriculture, Dorper (DOR), Katahdin (KAT), and St. Croix (STC) have become major hair sheep breeds in the U.S. (Thomas, 1991). However, despite the expansion of droughts due to climate change, no published reports involving direct comparisons of those breeds under controlled experimental conditions were found. Thus, we evaluated responses of DOR, KAT, and STC sheep originating from 4 distinct climatic regions of the U.S. to water restrictions at 75 and 50% of ad libitum intake and presented their performance results in a companion paper (Chapter III of this dissertation) suggesting that the 3 breeds had high resilience to limited water availability in the absence of heat stress. Because tolerance of small ruminants to limited water availability relies on physiological mechanisms they have developed to better cope with environmental stressors such as droughts (Parrot et al., 1996; Silanikove, 2000b; Chedid et al, 2014), it was necessary to elucidate whether the high resilience expressed by the 3 hair sheep breeds in performance had physiological bases. Thus, the objective of the current paper was to determine the sheep responses to the 75 and 50% water restriction treatments by evaluating a wide-range of blood characteristics and components sensitive to drinking water shortage.

MATERIALS AND METHODS

Animals and Treatments

The protocols for this experiment were approved by the Langston University Animal Care Committee. Forty-three DOR (initial BW = 60 ± 2.6 kg), 43 KAT (63 ± 2.4 kg), and 44 STC (45 ± 2.1 kg) sheep (3.5 ± 0.19 yr old) were used. The sheep were obtained from 45 commercial farms in the Midwest (MW; Iowa, Minnesota, Wisconsin, and Illinois), Northwest (NW; mainly Oregon and 2 farms in Washington), Southeast (SE; mainly Florida and 1 farm in southern Georgia), and central Texas (TX) regions of the U.S. and were used in a repeated measures experiment (Kuehl, 1999). The experiment consisted of 4 separate trials using 4 different sets of sheep that occurred in the spring (January-April) and summer (June-August) of 2016 and the spring (January-April) and summer (July-September) of 2017.

The 4 regions were chosen for their different climatic conditions using data from various computer programs such as Geographic Information System (GIS; Environment Rating Scales Institute, Redlands, CA) and National Ecological Observatory Network domains (NEON, Battelle Memorial Institute, Columbus, OH). The sheep breed associations for DOR, KAT, and STC were contacted, the zip codes of their members were geocoded (a process of converting addresses into geographical coordinates), and the geocoding for each breed was overlaid into the online NEON domains that were based on climate and geographical factors. Of the farms from which the sheep were obtained, one producer had two separate flocks and two had sheep of 2 breeds of different flocks. Before the onset of each trial, the sheep were vaccinated against clostridial organisms with Covexin® 8 (Schering-Plough Animal Health, Kenilworth, NH). The FAMACHA© score (van Wyk and Bath, 2002) determined at that time did not suggest a need for treatment for internal parasites.

The sheep were housed in a well-ventilated room individually in 1.05 × 0.55 m elevated pens with a plastic–coated expanded metal floor and each pen was fitted with a plastic barrel for feed and a bucket for water. Fecal and urinary excretions were removed and an odor absorbent was dispensed on the floor under pens daily.

Weather data were obtained from the Oklahoma Mesonet Guthrie station. The Oklahoma Mesonet, a network of environmental monitoring stations across Oklahoma, is maintained by the University of Oklahoma and Oklahoma State University. Mesonet measures air temperature and relative humidity at 1.5 m above ground using a thermistor-sortion probe (Campbell Scientific, Inc., Logan, UT) as described by Brock et al. (1995). Data downloaded were hourly temperature and relative humidity conditions at Langston University for the dates of each of the 4 trials of the experiment. These data were used to calculate heat load index (HLI) according to Gaughan et al. (2010): $HLI = 8.62 + (0.38 \times RH) + (1.55 \times BG) - (0.5 \times WS) + e^{(2.4 - WS)}$, whereas RH = relative humidity (%), BG = black globe temperature (ºC), WS = wind speed (m/s; assumed zero), and e = base of the natural logarithm. Those data were also used to calculate the temperature-humidity index (THI) according to Amundson et al. (2006): $THI = (0.8 \times {}^{o}C) + (RH/100) \times ({}^{o}C - 14.4) + 46.4$. Averages for temperature, RH, HLI, and THI outside the animal room were summarized across the 4 trials for the 3 experimental periods of drinking water availability and are presented in Table 1. The temperature and RH inside the animal room were also recorded every 1 h using a temperature and humidity monitor (Hobo®Temperature/RH Data Logger, model number U12-011; Onset Computer Corp., Bourne, MA). The temperature and RH records for the second trial (summer of 2016), however, were lost due to a malfunction of the instrument used. Thus, averages for temperature, RH, HLI, and THI inside the animal room were summarized across the 3 remaining trials and presented in Table 1.

The sheep were fed a pelleted diet (Table 2) at 71 g of dry matter (DM) per kg of metabolic body weight ($BW^{0.75}$) to meet approximately 160% of the metabolizable energy requirements for maintenance (NRC, 2007). There were 2 daily meals of equal amounts at 0800 and 1500 h, but the time of feeding on Wednesday mornings was 1 h later due to collection of blood samples before feeding. The amounts of feed offered were recorded and orts were weighed daily at 0800 h and used to calculate daily DM intake (DMI) by each animal. All sheep were weighed 3 times weekly (Monday, Wednesday, and Friday) at 1300 h to monitor change in BW throughout each trial. After weighing, half of the sheep were allowed access to an open floor area for 2 h before returning to their pens, an arrangement that provided an average of 3 h of group socialization each week.

The first 2 wk of each 9-wk trial served as a baseline period (period 1) during which time all sheep had free access to water. Ad libitum water intake (WI) was determined by filling the water buckets to capacity twice daily (0700 h and 1500 h) and weighing the remaining water at 0600 h the following day. Average WI by each animal over the 2-wk baseline period was then used as the estimate of ad libitum intake. Following the baseline period, all animals were offered water at 75% of ad libitum intake for 2 wk (period 2). Water was offered once daily at 0730 h and was consumed in a relatively short time. Next, water was restricted to 50% of ad libitum intake for 5 wk and was offered once daily at 0730 h (period 3). During this period, the sheep were expected to adapt to this level of restriction by conserving more water. At the end of those 5 wk, the sheep entered a rehydration phase by gradually bringing WI back to ad libitum by increasing the amount offered by 10% of ad libitum intake every 2 d and offering the water in 4 equal portions throughout the day (i.e., 0730, 0830, 1430, and 1530 h) to prevent hemolysis.

The protocol used for dehydration and rehydration of the sheep and selection of the water restriction treatments were based on the results of an initial study in our laboratory where the effects of restricting WI by KAT sheep and Boer and Spanish goats to 90, 80, 70, 60, 50, and 40% of ad libitum for 1 or 2 wk each were evaluated (Mengistu et al., 2016). Because there were minor physiological response differences (e.g., cortisol concentration) or no differences between the 50% and 40% restriction levels, the 50% of ad libitum WI was determined as an appropriate level for maximum water restriction in evaluations of resilience to limited water availability. It was also determined that a length of 2 wk rather than 1 wk for a water restriction level would be more appropriate in terms of increasing the meaningfulness of the measurements evaluated.

Sample Collection and Analysis

Representative samples of the pelleted diet were collected daily and stored at room temperature. Weekly composite samples were formed and ground to pass through a 1-mm screen and analyzed for DM and ash (AOAC, 2006), nitrogen (Leco TruMac CN, St. Joseph, MO), gross energy using a bomb calorimeter (Parr 6300; Parr Instrument Co. Inc., Moline, IL), and neutral detergent fiber (Van Soest et al., 1991) using an ANKOM200 Fiber Analyzer (filter bag technique; ANKOM Technology Corp., Fairport, NY).

Blood samples were collected twice weekly (Wednesday at 0800 h and Thursday at 1400 h) by jugular venipuncture into vacuum tubes with and without heparin for harvesting plasma and serum, respectively. By bleeding at 2 different times, potential differences in various measurements in whole blood and plasma as well as concentrations of serum metabolites between mornings and afternoons were assessed. Blood tubes were placed on ice and heparinized blood samples were immediately analyzed for hemoglobin (Hb) concentration and O_2 saturation using a Radiometer OSM 3 Hemoximeter™ (Kestrel Labs, Inc., Boulder, CO). Oxygen concentration was calculated as described by

Eisemann and Nienaber (1990) and packed cell volume (PCV) was measured in heparinized blood (Oladele et al., 2008) using a BD Microhematocrit centrifuge (Clay Adams, Parsipany, NJ). Plasma and serum were harvested by centrifugation of heparinzed and clotted blood samples, respectively, at 1,000 × *g* for 15 min and the plasma was immediately analyzed for osmolality by freezing point depression using an µ OSMETTE™ model 5004 osmometer (Precision System Inc., Natick, MA). Plasma and serum samples were then stored at –20 ^{o}C for later analyses. Serum concentrations of albumin, cholesterol, creatinine, glucose, lactate, total protein, triglycerides, and urea were determined using a Vet Axcel Chemistry Analyzer (Alfawassermann Diagnostic Technologies; West Caldwell, NJ). The concentrations of these serum metabolites were determined only in the blood samples collected at 1400 h in wk 2 of period 1, wk 2 of period 2, and wk 2, 4, and 5 of period 3. Using wk 2 was to assure adaptation of the sheep to the water level offered in each period, whereas wk 4 and 5 of period 3 were used to assure that the sheep were fully adapted to the severe water restriction of 50% of ad libitum intake. As to the 1400 h of blood sampling, it was chosen to assess the impact of dehydration as at least 6 h had passed since the sheep were offered and consumed their daily water allotments.

Statistical Analysis

Data were analyzed with mixed effects models using the MIXED procedure of SAS (Littell et al., 1996; SAS, 2013). Different statistical models were used for the different response variables measured in the whole blood, plasma, and serum samples collected from the sheep over time and each response variable was analyzed in multiple ways. To analyze response variables such as plasma osmolality and blood PCV, Hb concentration, O_2 saturation, and O_2 concentration during the baseline period, the statistical model included the fixed effects of set, breed, region, time of blood sampling, breed × region, breed × time, region × time, and the breed × region × time interaction with animal considered as a random effect and age as a covariate. To analyze differences in serum metabolites (i.e., albumin, cholesterol, creatinine, glucose, lactate, total protein, triglycerides, and urea) during the baseline period, the model included the fixed effects of set, breed, region, and the breed × region interaction with animal as a random effect and age as a covariate.

To analyze changes in plasma osmolality and blood PCV, Hb concentration, O_2 saturation, and O_2 concentration across the 3 experimental periods, the model included the fixed effects of set, breed, region, period, week within period, time of sampling, breed × region, breed × period, breed × week, breed × time, region × period, region × week, region × time, period × week, period × time, week × time, breed × region × period, breed × region × week, breed × region × time, breed × period × week, breed × period × time, breed × week × time, region × period × week, region × period × time, region × week × time, period × week × time, breed × region × period × week, breed × region × period × time, breed × region × week × time, breed × period × week × time, region × period × week × time, and the breed × region × period × week × time interaction with animal considered as a random effect and age as a covariate. To analyze changes in serum metabolites across periods, the model included the fixed effects of set, breed, region, period, week within period, breed × region, breed × period, breed × week, region × period, region × week, period × week, breed × region × period, breed × region × week, breed × period × week, region × period × week, and the breed × region × period × week interaction with animal considered as a random effect and age as a covariate. For these analyses, only the first 2 wk of data in period 3 were used so that periods were of the same length.

To analyze changes in plasma osmolality and blood PCV, Hb concentration, O_2 saturation, and O_2 concentration across the 5 wk of period 3, the model included the fixed effects of set, breed, region, week, time of blood sampling, breed × region, breed × week, breed × time, region × week, region × time, week × time, breed × region × week, breed × region × time, breed × week × time, region × week × time, and the breed × region × week × time interaction with animal considered as a random effect. Age and initial values taken during period 1 (baseline) also served as covariates in the model for each response variable. To analyze changes in serum metabolites across the 5 wk of period 3, the model included the fixed effects of set, breed, region, week, breed × region, breed × week, region × week, and the breed × region × week interaction with animal considered as a random effect. Age and initial values taken during period 1 (baseline) also served as covariates for each response variable.

An average for each response variable was taken during the last 2 wk of period 3 because this was when animals were expected to be adapted to the 50% water restriction. These values were used to evaluate the relationships between variables reflecting resilience to limited water availability and genetic characteristics. For plasma osmolality and blood PCV, Hb concentration, O_2 saturation, and O_2 concentration, the model included set, breed, region, time of blood sampling, breed × region, breed × time, region × time, and the breed × region × time interaction as fixed effects and animal as a random effect with age and baseline values as covariates. The model used to analyze changes in serum metabolites during the last 2 wk of period 3 included set, breed, region and the breed × region interaction as fixed effects and animal as a random effect with age and initial values taken during period 1 (baseline) as covariates.

Means were separated using the LSMEANS statement and pairwise comparisons were conducted using Fischer's LSD (PDIFF option). Statistical significance was declared at $P < 0.05$. It is worth noting that each of the sheep breeds used in the study represented the 4 climatic regions to examine the effects of relatively distinct regions with different climatic conditions on resilience to limited water availability. This was also done so that the U.S. populations of the 3 hair sheep breeds would be adequately represented. Considering that the number of sheep per breed and region were not exactly equal, the 3-way interaction means were presented to help explain main effects and 2-way interaction means, with greater attention given to breed and region effects.

Spearman's rank correlation coefficients (*sr*) were determined using the CORR procedure of SAS to evaluate consistency in the ranking of response variables among the 3 periods and among the 5 wk of period 3 within each hair sheep breed and overall for plasma osmolality, blood PCV, and blood Hb concentration at each sampling time. To assess variability among breeds at each sampling time for a response variable during water restriction, Bartlett's test for homogeneity of variance was performed using the GLM procedure of SAS.

RESULTS AND DISCUSSION

Physiological Responses to Limited Water Availability

Under pervasive environmental stressors such as rising environmental temperatures or expansion of droughts, ruminants developed physiological mechanisms to adapt to such harsh conditions (Silanikove, 1992; Parrot et al., 1996; Silanikove, 2000b) and improve their water economy by decreasing urine excretion and producing dry feces through vasopressin's actions on the kidneys and the gastrointestinal tract (Olsson, 2005). An example of this adaptation was demonstrated in Awassi sheep, a fat-tailed Middle Eastern breed known for resilience to water shortage, by depriving them of water for 5 d after offering them water ad libitum (Laden et al., 1987). On d 5, urine volume and fecal water content decreased from 1,278 to 120 mL/d and from 52.6 to 11.9%, respectively, whereas urine osmolality and urea concentration increased from 1,352 to 1,924 mosm/L and from 340 to 5,425 mg/dL, respectively. Plasma osmolality and creatinine concentration also increased from 278 to 328 mosm/L and from 0.8 to 1.5 mg/dL, respectively. Despite these drastic changes, those sheep not only survived, but also were able to replace their water losses 1 d after being offered water ad libitum. The Awassi breed, however, represents an extreme example of adaptation as other breeds of sheep (Chedid et al., 2014) and goats (Silanikove, 2000b) exhibited less abilities to cope with drinking water shortage.

In general, dehydration leads to hemoconcentration due to decreased plasma volume as water is taken up by tissue cells, including red blood cells (Schaefer et al., 1990). However, the decrease in plasma volume varies with the severity of drinking water shortage. Depriving DOR rams in an Israeli desert of water for 4 d while being offered only wheat straw decreased BW, total body water volume, extracellular fluid volume, and plasma volume by 16.3, 22.0, 35.1, and 41.7%, respectively (Degan and Kam, 1992). A consequence of decreased plasma volume and increased renal retention is hyperosmolality along with increased electrolyte concentrations (Qinisa et al., 2011). The processes by which animals attempt to cope with water shortage and preserve homeostasis, including the rumen important role as a water reservoir to replenish the losses in plasma volume, are described by Silanikove (1994).

Many breeds of sheep (Aganga et al., 1989; Hamadeh et al., 2006; Kumar et al., 2016) and goats (Alamer, 2006; Mengistu et al., 2007a; Kaliber et al., 2016) have exhibited various degrees of resilience to shortages of drinking water, especially in arid and semiarid regions. This resilience was demonstrated in studies evaluating infrequent watering strategies to simulate management conditions under which small ruminants travel long distances in search of feed and water which deprives them of water for days. Examples included offering water to sheep every 3 d (Aganga et al., 1989; Hamadeh et al., 2006), 4 d (Jaber et al., 2004; Ghanem et al., 2008), or 5 d (Igbokwe, 1993) and to goats every 3 d (Alamer, 2006) or 4 d (Mengistu et al., 2007a,b). Resilience was also demonstrated in a few studies evaluating restrictions of the amount of water offered daily to sheep (De et al., 2015; Kumar et al., 2016; Vosooghi-Postindoz et al., 2018) or goats (Ahmed and El Kheir, 2004; Alamer, 2009; Kaliber et al., 2016) at levels ranging from 40 to 60% of ad libitum intake. In those studies and others, assessment of the physiological responses to water restriction involved monitoring certain blood characteristics and serum metabolites that reflect the ability of the affected animals to cope with the stress caused by water shortage. In addition to elevated plasma osmolality, increased PCV and Hb concentration are considered good indicators of dehydration in sheep (Laden et al., 1987; Abdelatif and Ahmed, 1994; Ghanem et al., 2008) as the former is a measure of red blood cells and the latter is a structural component of red blood cells. However, no changes in those measurements were found in other dehydrated sheep (Aganga et al., 1989; Igbokwe, 1993; Jaber et al., 2004). Although increased Hb concentration in sheep was attributed to decreased plasma volume (Li et al., 2000; Hamadeh et al., 2006), the contradictory results suggest that adapted sheep can maintain plasma volume during periods of water shortage. Finally, blood O_2 saturation and O_2 concentration are considered in the present study as potential indicators of water restrictions due to their association with Hb and its ability to meet O_2 demand.

Of the serum metabolites, urea is mainly synthesized in the liver using ammonia, released to the blood, and excreted by the kidneys to dispose of endogenous and excess dietary nitrogen or recycled through saliva and reabsorption into the rumen to be utilized by rumen bacteria (Huntington and Archibeque, 2000). As to creatinine, it is produced in the muscles and excreted by the kidneys in proportion to the muscle mass and the rate of proteolysis (Caldeira et al., 2007a). But under water restriction, the transfer function of the kidney is altered (Kataria and Kataria, 2007) with slower glomerular filtration and higher urea reabsorption (Silanikove, 2000b; Marini et al., 2004). As a result, blood concentrations of urea and creatinine are increased in sheep under water restriction (Laden et al., 1987; Igbokwe, 1993; Jaber et al., 2004). According to Caldeira et al. (2007a,b), serum concentrations of total protein and albumin are good predictors of the animal's protein status and a decrease in albumin concentration is common in ruminants suffering from prolonged low dietary protein intake (Caldeira et al., 2007a). This is because serum albumin serves as a labile protein reservoir of readily available amino acids until other source is made available through the diet or mobilization of endogenous sources such as skeletal muscles (Moorby et al., 2002). Because albumin plays an important role in osmoregulation and control of fluid movement between different body compartments, its breakdown and synthesis are regulated in response to dehydration to maintain normal colloid osmotic pressure and fluid distribution (Burton, 1988). Considering these physiological functions, the reported decreases in concentrations of total protein and albumin in sheep were attributed to low DMI caused by water restriction (El-Sherif and Assad, 2001; Hamadeh et al., 2006). However, increases in concentrations of total protein and albumin have been consistently reported in water-restricted sheep (Jaber et al. 2004; Casamassina et al., 2008; Ghanem et al., 2008) and were attributed to decreased blood volume caused by water restriction (Degan and Kam, 1992). Similar to other serum metabolites, contradictory results were found for glucose concentrations with either decreases (Annison and White, 1961) or no change (Igbokwe, 1993; Jaber et al., 2004; Casamassima et al., 2008) in water-restricted sheep. Because ingested carbohydrates are efficiently fermented to volatile fatty acids in the rumen, circulating glucose in ruminants is derived from propionate and other non-carbohydrate precursors (e.g., lactate, glycerol, and amino acids) through gluconeogenesis (Baird et al., 1980). However, as gluconeogenesis is inhibited by reduced propionate production in the rumen in response to low DMI (Allen et al., 2009), it is anticipated that the negative effect of dehydration on DMI would influence serum glucose concentrations. As a key gluconeogenic substrate, circulating lactate is an end product of fermentation in the gastrointestinal tract or nonoxidative glycolysis in the tissues (Woerle et al., 2003). In either case, serum lactate concentrations could be influenced by water restriction considering that a major portion of circulating lactate (up to 70%) is subject to renal tubular reabsorption (Ewaschuk et al., 2005). Finally, concentrations of cholesterol and triglycerides are considered good indicators of drinking water shortage. Increased serum concentrations of cholesterol (Umunna et al., 1981; Igbokwe, 1993; Jaber et al., 2004) and triglycerides (Casamassima et al., 2008, Nejad et al., 2014) in water-restricted sheep have been attributed to decreased DMI and the subsequent need for fat mobilization to meet the shortfall in energy requirements (Chedid et al., 2014).

Experimental Considerations

To our knowledge, the present study is the first to directly evaluate physiological responses of different sheep breeds from different climatic regions to water restriction. Knowing that environmental, animal, and dietary factors can influence animals' response to water restriction, that previous studies varied in the type of water restrictions tested, and that most of them compared water-restricted animals to others having ad libitum access to water, key considerations were taken into account in the design and protocols used in this study.

First, the fact that most water restriction studies tested infrequent watering regimes applicable to certain arid or semiarid regions and to local breeds of sheep or goats, their recommendations may not be applicable to other regions where water is available, but limited due to climate change. Also, the resilience unique to those breeds could make infrequent watering impractical and potentially dangerous to breeds adapted to less harsh or temperate environments. For these reasons, we examined daily water restrictions levels that, if tolerable, could be adopted universally in cases of water shortage without fear for animal health or wellbeing. In doing so, we used hair sheep breeds not only well adapted to the adverse climates of arid and tropical regions but also have been increasing in numbers and becoming more attractive in many countries (Rowe, 2010; Silva et al., 2004; Sánchez-Dávila1 et al., 2015), including the U.S. (Thomas, 1991; Wildeus, 1997; Notter, 2000).

Second, in most studies evaluating resilience to limited drinking water availability, the level of restriction was not based on ad libitum WI (baseline) by the same sheep (Casamassima et al., 2008, 2016; Kumar et al., 2016) or goats (Kaliber et al., 2016). Instead, the restricted levels were determined as proportions of WI by groups of similar animals having ad libitum access to water. Such an arrangement does not consider actual ad libitum intake by the animals being subjected to water restriction (i.e., individual animal variability), which could negatively affect the results. In contrast, the present study was designed to include a 2-wk baseline period during which all sheep were offered water ad libitum and both the initial and final restriction levels used (75 and 50%, respectively) were determined for each sheep based on its own ad libitum WI.

Third, based on the results of our water-restriction study with KAT sheep and Boer and Spanish goats (Mengistu et al., 2016), the present study was designed to offer the sheep water at 100, 75, and 50% of ad libitum intake in 3 sequential periods lasting 2, 2, and 5 wk, respectively. Furthermore, in order to assess change in blood measurements across the 5 wk of period 3 with the 50% water restriction level, the initial values obtained during the baseline period along with animal age served as covariates in the statistical model used to evaluate resilience.

Fourth, considering that THI is the most effective and commonly used index to evaluate effects of heat stress on ruminants (Gaughan et al., 1999; Nasr and El-Tarabany, 2017), it was calculated for the sheep used in this study. The results (Table 1) for outside (across the 4 trials) and inside (across 3 trials) the room where the sheep were kept showed that THI ranged from 43.3 to 48.5 and from 45.1 to 46.4, respectively, whereas HLI, another heat stress index, ranged from 69.0 to 73.2 and from 70.4 to 74.3, respectively. Studies on heat stress suggested a THI ≤ 74 as a comfort threshold for beef cattle (Hahn et al., 2009) and a THI < 65 as a comfort threshold for dairy cattle (Silankove and Koluman, 2015). Using hair sheep breeds other than those evaluated in the present study, Seixas et al. (2017) demonstrated that in Brazil, Santa Inês and Morada Nova sheep were thermally comfortable at THI averaging 59 and 61 but suffered heat stress at higher THI values such as 79. In our laboratory, KAT sheep were shown to be in thermal comfort at THI of 64.5 and at HLI of 66 and began to exhibit signs of heat stress at THI > 74 and HLI > 75 (Mengistu et al., 2017). These results demonstrated that heat stress was not a factor as our sheep were within their comfort threshold.

Finally, in addition to assuring comfort of the sheep used in the 4 trials, possible confounding factors concerning performance were also avoided by using sheep that were neither pregnant nor lactating and had ad libitum access to a balanced diet (Table 2) that met and exceeded their maintenance requirements (NRC, 2007).

Baseline Period

Because no significant interactions between or among breed, region, and time of blood sampling were detected for blood characteristics when water was offered ad libitum during the 2-wk baseline period (Table 3), main effect means are presented in Table 4. Plasma osmolality was lower ($P < 0.05$) for DOR than for KAT and STC sheep, which had similar ($P > 0.05$) values. Osmolality, however, was not affected ($P > 0.05$) by region and neither the breed nor region affected ($P > 0.05$) blood PCV, Hb concentration, O_2 saturation, or O_2 concentration. In contrast, the effect of time of sampling was significant as plasma osmolality was higher ($P < 0.05$) at 1400 h than at 0800 h, whereas PCV, Hb concentration, O_2 saturation, and O_2 concentration were higher ($P < 0.05$) at 0800 h. Tables 5 and 6 showed no significant breed × region interactions for or main effects on the serum metabolites measured except for cholesterol and triglycerides that were influenced by breed. Cholesterol concentration was higher ($P < 0.05$) for KAT than for DOR and intermediate ($P > 0.05$) for STC sheep. Concentration of triglycerides was also higher ($P < 0.05$) for KAT than for DOR or STC sheep which had similar ($P > 0.05$) values. Notably, the PCV values, Hb concentrations, and serum concentrations of albumin, cholesterol, creatinine, glucose, lactate, total protein, triglycerides, and urea when the sheep had ad libitum access to water in period 1 fell within the normal ranges reported for sheep (Hindson and Winter, 1996; Martin and Aitken, 2000; Cork and Halliwell, 2002). Plasma osmolality values and both saturation and concentration of O_2 also fell within the normal ranges for sheep (Mengistu et al., 2016).

Except for the study of Mengistu et al. (2016) where KAT wethers were used, no osmolality data were reported for the hair sheep breeds evaluated in the present study. Considering the similarity in offering KAT sheep water ad libitum in a 2-wk baseline period, the higher osmolality in those wethers than in our KAT sheep (304 vs 302.1 mosm/L) could be due to using younger animals (1-yr vs. 3.5-yr old) and keeping them under a higher range of environmental temperatures (19.1 to 29.8 ^{o}C vs. 13.6 to 23.4 8 ^{o}C) than ours. These factors could also explain the differences between the morning and afternoon plasma osmolality values for KAT sheep in the present study (300.2 vs. 303.0 mosm/L at 0800 and 1400 h, respectively) versus those (300 vs. 311 mosm/L at 0700 and 1300 h, respectively) in the study of Mengistu et al. (2016). In that study, higher PCV and

O_2 concentration were detected in the morning than in the afternoon, a response similar to that for PCV, Hb and O_2 concentrations, and O_2 saturation in our sheep. It is possible that the higher plasma osmolality detected in the afternoon could have resulted from increased body water loss through evaporative cooling mechanisms, including panting, and the resulting increase in plasma osmolality due to rising ambient temperatures. The greater PCV and Hb in the morning, however, may have been caused by lack of water absorption from the rumen immediately after water was offered in the morning.

The higher serum concentrations of cholesterol and triglycerides in KAT than in DOR or STC sheep could be explained by the tendency of the KAT breed to have more fat depots than other hair sheep. When growing lambs of three hair sheep breeds, including KAT and STC, were offered feed and water ad libitum for 94 d and evaluated for performance and carcass characteristics, Horton and Burgher (1992) reported that KAT lambs had a higher cholesterol concentration (53.3, 39.7, and 49.8 mg/dL, respectively) than STC or Barbados Blackbelly lambs and attributed the response to the greater fat content of KAT lamb carcasses than those of the other breeds (i.e., 11.8, 6.2, and 5.5% for KAT, Barbados Blackbelly, and STC respectively). The higher cholesterol concentration in our KAT sheep (67.1 mg/dL), however, may reflect the fact that our mature sheep had accumulated more fat depots. Similar to our findings, no differences in plasma concentrations of albumin, glucose, or urea were found between KAT and STC sheep (Horton and Burgher, 1992).

Period Comparisons

The *P* values for the main effects of and interactions among breed, region, period, week within period, and time of blood sampling as to the blood characteristics are presented in Table 7 with the corresponding means in Table 8 and Fig. 1 to 8. No significant 5-way or 4-way interactions were found for any of the blood characteristics evaluated. However, there were significant 3-way interactions for some and are presented as breed × region × period interaction plots for PCV (Fig. 1) and O_2 saturation (Fig. 2) and as period × week × time interaction plots for plasma osmolality (Fig. 3), PCV (Fig. 4), and O_2 saturation (Fig. 5).

The breed × region × period interaction for PCV seemed to have resulted from large region differences among DOR sheep with those from the NW and SE having the lowest ($P < 0.05$) PCV and those from the MW and TX having the highest ($P < 0.05$) PCV under the 75 and 50% water restrictions in periods 2 and 3, respectively (Fig. 1; Panel A). In contrast, PCV for KAT and STC sheep consistently increased ($P < 0.05$) with advancing water restriction regardless of their origin (Fig. 1; Panels B and C, respectively). The only exception was that PCV for STC sheep from the MW decreased ($P < 0.05$) under the 50% water restriction. As to the breed × region × period interaction for O_2 saturation, the levels for DOR and KAT sheep from the NW decreased ($P < 0.05$) and the levels for sheep of the same breeds from the other regions increased ($P < 0.05$) with advancing water restriction (Fig. 2; Panels A and B). In contrast, O_2 saturation decreased ($P < 0.05$) in STC sheep from the MW and SE and increased ($P < 0.05$) in STC from the other regions with advancing water restriction (Fig. 2; Panel C). Although, there is no clear explanation for such different responses to water restriction, these observations underscore the influence of breed and origin on the sheep ability to physiologically adapt to limited water availability. It is worth noting that no published reports addressing the effect of region of breed on responses of small ruminants to water restriction were found.

The period × week × time interactions detected for plasma osmolality and blood PCV and O_2 saturation reflected differences in time of blood sampling and showed how all sheep, regardless of their breed or region, responded to the water restriction treatments. Across periods, osmolality was higher ($P < 0.05$) at 1400 h than at 0800 h in wk 1 but the values decreased ($P < 0.05$) in wk 2 and resulted in similar ($P > 0.05$) values for both times in period 3 (Fig. 3). Notably, the greater osmolality at 1400 h than at 0800 h reflected the impact of dehydration as at least 6 h had passed since the sheep were offered and consumed their daily water allotments. Greater plasma osmolality values in the afternoon than in the morning were also reported for KAT sheep and Boer and Spanish goats offered water at 100, 70, and 50% of ad libitum intake for 2 wk each (Mengistu et al., 2016). The corresponding osmolality values across species were 300, 303, and 315 mosm/L at 0700 h and 312, 316, and 322 mosm/L at 1300 h, respectively. The greater osmolality values for the afternoon blood samples in the study of Mengistu et al. (2016) than in ours, especially at 50% water restriction (322 vs. 310 mosm/L), could be attributed, in part, to the use of younger animals that were kept under higher environmental temperatures than our mature sheep and suggests that the wethers may have been less able to cope with the severe water shortage. In contrast to plasma osmolality, PCV (Fig. 4) was lower ($P < 0.05$) at 1400 h than at 0800 h in wk 1 and 2 of each period except for wk 2 of period 3 in which the sheep had similar ($P > 0.05$) PCV values. According to Hindson and Winter (1996) and Martin and Aitken (2000), the normal range for PCV in sheep is 22-40%, while Cork and Halliwell (2002) reported a normal range from 24-50%. Average PCV values for wk 1 and 2 were 32.2, 32.4, and 32.8% at 0800 h and 31.0, 31.4, and 32.0% at 1400 h when the sheep offered water at 100, 75, and 50% of ad libitum intake, respectively. Mengistu et al. (2016) also reported greater PCV values at 0700 h (26.5, 26.2, and 24.2%) than at 1300 h (26.3, 25.5, and 24.0%) for KAT sheep and Boer and Spanish goats offered water at 100, 70, and 50% of ad libitum intake for 2 wk each, respectively. The similar osmolality (Fig. 3) and PCV (Fig. 4) detected at both times of blood sampling in wk 2 of period 3 suggests that regardless of breed or region, the sheep needed 1 wk for developing mechanisms to cope physiologically with the 50% water restriction. As to O_2 saturation (Fig. 5), it fluctuated without a clear effect of period, week, or time except for that the saturation levels in the morning and in the afternoon were similar ($P > 0.05$) in wk 2 of the 75 and 50% water restrictions (66.9 and 70.7%, respectively). In the study of Mengistu et al. (2016), however, O_2 saturation was higher in the afternoon of wk 2 for the 50% than for the 70% water restriction (averaging 77.0 vs. 72.0%). Nevertheless, these results underscore the importance of increased O_2 saturation as an adaptation mechanism to cope with dehydration in order to meet the O_2 demand, especially when PCV values were consistently lower in the afternoon than in the morning.

Four significant 2-way interactions were detected for osmolality (Fig. 6, 7, and 8) and for PCV (Table 8) and displayed differences among the sheep breeds, among the regions, and between wk 1 and 2 of each period in coping with advancing water restriction. A breed × period interaction for osmolality (Fig. 6) showed that it increased ($P < 0.05$) as period advanced, with lesser change from period 1 to 2 for STC compared with the other breeds. It also showed greater ($P < 0.05$) osmolality values for KAT than for DOR in each period and for STC in periods 2 and 3. Even though osmolality for the DOR, KAT, and STC sheep slightly differed in period 1 (300, 302, and 303 mosm/L, respectively) increased differently in period 2, and plateaued in period 3 (308, 309, and 308 mosm/L, respectively). A breed × period interaction for PCV (Table 8) also showed differences among breeds in that the highest ($P < 0.05$) value was for STC sheep in period 3 and the lowest ($P < 0.05$) for KAT sheep in period 2. Considering both interactions, it is evident that under 50% water restriction all sheep maintained an average osmolality of 308 mosm/L, which is only 6 mosm/L more than their average osmolality while having ad libitum access to water. It is also evident that the sheep had similar ($P > 0.05$) PCV values in period 3 averaging 32.4%, which is only 0.8 percentage unit more than their average PCV while having ad libitum access to water. Thus, these results suggest that the 3 hair sheep breeds were equally resilient to such a severe shortage in drinking water. A region × period interaction (Fig. 7) showed that sheep from all regions had similar ($P > 0.05$) osmolalities in period 1 (averaging 301.5 mosm/L) that increased ($P < 0.05$) to similar ($P > 0.05$) values in period 2 (averaging 304.5 mosm/L) and increased ($P < 0.05$) further in period 3 where sheep from the MW, NW, and SE, which did not differ, had greater ($P < 0.05$) values than that for sheep from TX (averaging 309.3 vs. 307.0 mosm/L). Although these observations reflected the impact of water restriction, they suggested the sheep from TX to be better adapted to severe water shortage. Finally, a period × week interaction (Fig. 8) showed that all sheep had similar ($P > 0.05$) osmalalities in wk 1 and 2 of period 1 that increased ($P < 0.05$) with advancing water restriction, but to levels that were lower ($P < 0.05$) in wk 2 (303 and 307 mosm/L) than in wk 1 (306 and 310 mosm/L) of periods 2 and 3, respectively. This observation suggests that regardless of breed or region, the sheep needed 1 wk to adapt to each of the water restriction treatments. It also suggests that adaptation to limited water availability had been achieved by decreasing water losses as demonstrated in the modest change in plasma osmolality.

The breed effects on variables not involved in interactions are presented in Table 8. The results showed that all breeds had similar ($P > 0.05$) Hb concentrations (averaging 12.12 g/dL) but STC had higher ($P < 0.05$) O_2 saturation (71.9 vs. 65.9%) and O_2 concentration (11.77 vs. 10.65 mmol/L) than DOR or KAT sheep which had similar ($P > 0.05$) values. Studies examining the effects of water restrictions on small ruminant breeds have been limited to goats (Alamer et al., 2006; Qinisa et al., 2011; Mengistu et al., 2016). Depriving Hipsi, Aardi, and Zumri goats (Saudi Arabian breeds) of water for 3 d did not show a breed effect on plasma osmolality or PCV except for Zumri that maintained greater PCV values each day than those of the other breeds (Alamer, 2006). Restriction of daily WI to 50% of ad libitum for 7 d resulted in greater PCV and lower plasma total protein concentration in Tswana than in Boer goats without affecting plasma osmolality or urea concentration (Qinisa et al., 2011). Mengistu et al. (2016) reported that offering Boer and Spanish goats water at 100, 90, 80, 70, 60, 50, and 40% of ad libitum intake for 1 or 2 wk each did not show breed effect on plasma osmolality, PCV, or O_2 saturation across treatments (averaging 312.5 mosm/L, 22.6%, and 71.0%, respectively), but Boer goats had lower O_2 concentration than Spanish goats (3.39 vs. 4.02 mmol/L).

The *P* values for the main effects of and interactions among breed, region, and period as to the serum metabolites measured are presented in Table 9 with the corresponding means in Table 10. No significant breed × region × period, breed × period, or region × period interactions were found for any of the metabolites evaluated. However, there were significant breed × region interactions for albumin and creatinine that revealed differences among the sheep breeds regardless of the drinking water treatment. The DOR from the MW, KAT from the NW and SE, and STC from TX had the highest ($P < 0.05$) albumin concentrations (averaging 2.65 g/dL) whereas KAT from TX and STC from the MW had the lowest ($P < 0.05$) values (averaging 2.46 g/dL). These albumin values were within the normal range (2.4-3.5 g/dL) for sheep (Hindson and Winter, 1996; Martin and Aitken, 2000; Cork and Halliwell, 2002). Also, DOR and STC from the NW had the highest ($P < 0.05$) and lowest ($P < 0.05$) creatinine concentrations (1.049 vs. 0.740 mg/dL), respectively, and DOR maintained higher ($P < 0.05$) creatinine concentrations than STC in each of the 4 regions. Although these differences are interesting and consistent, especially for DOR and STC sheep, they are difficult to explain. Hence, the breed means for serum concentrations of albumin and creatinine are presented in Table 10 even though there were breed × region interactions for those measurements. While albumin concentrations were similar ($P > 0.05$) for the 3 breeds, those breeds differed ($P < 0.05$) in creatinine concentrations with DOR > KAT > STC.

As to the other serum metabolites measured but not involved in interactions, they were not affected ($P > 0.05$) by the sheep breed or region except for concentration of triglycerides that was higher ($P < 0.05$) for KAT (34.8 g/dL) than for DOR or STC sheep which had similar ($P > 0.05$) values (averaging 29.1 g/dL). These serum triglyceride concentrations were within the normal range (7.7-38.7 mg/dL) for sheep (Martin and Aitken, 2000). Notably, there were significant period effects on all serum metabolites except lactate, but the sheep responses to restricting WI to 75% of ad libitum in period 2 were variable when compared with their baseline (period 1) responses. While urea concentration increased ($P < 0.05$), concentrations of albumin, glucose, and total protein decreased ($P < 0.05$) and concentrations of cholesterol, creatinine, and triglycerides did not differ ($P > 0.05$) from the baseline levels. However, concentrations of albumin, cholesterol, creatinine, glucose, triglycerides, and urea were consistently highest when WI was restricted to 50% of ad libitum in period 3. The corresponding increases above baseline concentrations were 3.5, 25.0, 15.7, 7.6, 21.9, and 15.5%, respectively. Interestingly, total serum protein concentrations for sheep under 50% water restriction and ad libitum WI did not differ ($P > 0.05$).

Weekly Changes During Period 3

In a companion paper (Chapter III of this dissertation), the resilience of the 3 hair sheep breeds to water restriction to 50% of ad libitum intake was established based on their performance, especially that during the 5 wk of period 3. First, the sheep DMI in those 5 wk of severe water restriction decreased only by 8.8% of their DMI when offered water ad libitum in the baseline period, a reduction considered minor relative to those reported for small ruminants under 50% water restriction. Examples included reductions in DMI of 22% for Aardi does over 6 d (Alamer, 2009) and of 40 and 42% for Baluchi lambs over 42 d on water low or high in total dissolved solids, respectively (Vosooghi-Postindozet al., 2018). Second, BW of most sheep was either stable or decreased in wk 1 (averaging 1.4% loss) but gradually increased in the remaining 4 wk of period 3 with gain ranging from 0.4% in wk 2 to 1.9% in wk 5). This performance displayed a clear resilience advantage for the 3 hair sheep breeds when compared with the reported decreases of 8% in BW of goats (Alamer, 2009) and of 64 and 75% in average daily gain of sheep (Vosooghi-Postindozet al., 2018). Third, the BW gain detected in period 3 was postulated to have resulted from increased DM digestibility and improved efficiency of energy utilization. Such digestive and metabolic improvements have been demonstrated under 50% water restriction in dairy cows (Steiger Burgos et al., 2001) and in STC sheep consuming the same pelleted diet in Chapter V of this dissertation. For these reasons, it was critically important to analyze the blood characteristics and serum metabolites data for period 3 alone to understand the physiological responses of the 3 hair sheep breeds from the 4 different climatic regions to the 50% water restriction.

The *P* values for the main effects of and interactions among breed, region, week, and time of blood sampling as to the blood characteristics are presented in Table 11 with the corresponding means in Tables 12 and 13 and in Fig. 9 to 15. Except for breed × region × week interactions for PCV and Hb concentration, no significant 4-way or 3-way interactions were found for any of the blood characteristics evaluated. Those significant breed × region × week interactions were primarily caused by the responses of DOR sheep from the NW. While most sheep maintained similar ($P > 0.05$) PCV values (Fig. 9) and Hb concentrations (Fig. 10) in each week of period 3, DOR from the NW consistently had the lowest ($P < 0.05$) values, a response suggesting that their blood volume was less influenced by the 50% water restriction than other sheep. The normal concentration for blood Hb in sheep ranges from 8-16 mg/dL (Hindson and Winter, 1996; Martin and Aitken, 2000; Cork and Halliwell, 2002) and none of the sheep in our study had Hb values outside that range.

As to the 2-way interactions, there were none between breed and region or between breed and time for any of the blood characteristics evaluated, but there were significant breed × week interactions for PCV, Hb concentration, and O_2 saturation (Table 12). The interactions for PCV and Hb concentration revealed the greatest (P < 0.05) values for STC sheep in wk 5 and the lowest (P < 0.05) values for KAT sheep also in wk 5. Both interactions also showed that across the 5 wk of period 3, PCV values and Hb concentrations were similar (P > 0.05) for each breed except for KAT where the values for wk 5 were different (P < 0.05) from those for wk 1. The breed × week interaction for O_2 saturation, however, showed different patterns with the highest (P < 0.05) level for STC in wk 3 and the lowest (P < 0.05) for KAT in wk 1. This interaction also showed that the saturation levels for each breed were similar (P > 0.05) across the 5-wk period except in wk 3 for STC and in wk 4 for DOR and KAT where their levels were different (P < 0.05) from their levels in wk 1.

Other 2-way interactions between region and week, region and time, and week and time were also significant for one or more of the blood characteristic evaluated. A region × week interaction was found for plasma osmolality (Fig. 11) and seemed to have been caused by deviations in certain sheep responses from the sharp decrease (P < 0.05) in osmolality over time as it steadily increased (P < 0.05) after wk 2 for the sheep from the NW and increased (P < 0.05) after wk 4 for those from the SE and TX. Nevertheless, there were consistent decreases in plasma osmolality from a range of 309 to 313 mosm/L in wk 1 to a range of 304 to 308 mosm/L in wk 2 to 5. This response suggests that regardless of region, all sheep needed 1 wk to adapt to the severe water shortage by lowering and stabilizing plasma osmolality. There were region × time interactions for osmolality and O_2 saturation (Table 13) that revealed similar (P > 0.05) osmolality for sheep from the NW at 0800 and 1400 h but greater (P < 0.05) osmolality for sheep from the other regions at 1400 h. In contrast, only sheep from the SE had a higher (*P* < 0.05) O_2 saturation level at 1400 h whereas sheep from the other regions had similar (*P* > 0.05) saturation levels at both times of blood sampling. Finally, there were week × time interactions for osmolality, PCV, Hb concentration, and O_2 saturation that showed different responses. In contrast to the fluctuation in osmolality at 1400 h over the 5-wk period, osmolality at 0800 h gradually decreased (*P* < 0.05) from wk 1 to wk 3 and then increased (*P* < 0.05) to a level in wk 5 that was not different (*P* > 0.05) from that in wk1 (Fig. 12). The interaction for PCV showed different (*P* < 0.05) values in wk 1, similar (*P* > 0.05) values in wk 2 and 5, and the highest (*P* < 0.05) and lowest (*P* < 0.05) values occurring in wk 3 at 0800 and 1400 h, respectively (Fig. 13). The interaction for Hb showed higher (*P* < 0.05) concentrations at 0800 h than at 1400 h in wk 1, 3, and 4, but similar (*P* > 0.05) concentrations in wk 2 and 5 (Fig. 14). The interaction for O_2 saturation, however, showed an opposite trend with higher (*P* < 0.05) saturation levels at 1400 h than at 0800 h in wk 1, 3, and 4, but similar (*P* > 0.05) levels in wk 2 and 5 (Fig. 15).

Finally, the main effects of breed and week on plasma osmolality and O_2 concentration (Table 12) showed that osmolality tended to be greater (*P* = 0.071) for KAT than for DOR or STC sheep and O_2 concentration was higher (*P* < 0.05) for STC than for DOR or KAT sheep which did not differ (*P* > 0.05). Osmolality was also greater (*P* < 0.05) in wk 1 than in the other 4 wk of period 3 during which the sheep had similar (*P* > 0.05) values and there was a trend for a higher (*P* = 0.05) O_2 concentration in wk 4.

The *P* values for the main effects of and interactions among breed, region, and week as to the serum metabolites are presented in Table 14 with the corresponding means in Table 15. No significant breed × region × week, breed × week, or region × week interactions were found for any of the metabolites measured. However, there was a significant breed × region interaction for creatinine showing that all sheep had similar ($P > 0.05$) concentrations except for DOR from the NW and STC from the NW and SE which had the highest ($P < 0.05$) and lowest ($P < 0.05$) concentrations, respectively, as they demonstrated differences in copying with the 50% water restriction. There were significant breed effects in that STC had a lower ($P < 0.05$) creatinine concentration and a higher ($P < 0.05$) glucose concentration than those for DOR or KAT sheep which had similar ($P > 0.05$) concentrations of each metabolite. As to the region effect, it was significant for cholesterol with the highest ($P < 0.05$) and lowest ($P < 0.05$) concentrations for sheep from the MW and NW, respectively, whereas sheep from the SE and TX had similar ($P > 0.05$) concentrations. There were significant week effects on several serum metabolites that showed differences among the 3 wk of period 3 (i.e., wk 2, 4, and 5) in which those metabolites were measured. Concentrations of albumin, cholesterol, and urea fluctuated in wk 2, but were higher ($P < 0.05$) in wk 4 than in wk 5. In contrast, concentrations of creatinine and glucose were highest ($P < 0.05$) in wk 2 and lowest ($P < 0.05$) in wk 5. Based on the results in Tables 12 and 15, it is evident that STC sheep had a resilience advantage over DOR and KAT sheep as they maintained the highest concentrations of O_2 (12.32 v. 11.17 mmol/L) and glucose (60.1 vs. 55.6 mg/dL) and the lowest creatinine concentration (0.868 vs. 0.943 mg/dL) while under 50% water restriction in period 3.

Changes During the Last Two Weeks of Period 3

As noted earlier, the data collected in the last 2 wk of period 3 were analyzed for possible changes when the sheep were fully adapted to the 50% water restriction. The *P* values for the main effects of and interactions among breed, region, and time of blood sampling as to the blood characteristics are presented in Table 16 with the corresponding means in Table 17 and Fig. 16. No significant breed × region × time interactions were found for any of the blood characteristics evaluated except for O_2 concentration that was highest ($P < 0.05$) for STC from the SE at 0800 h and TX at 1400 h (12.86 and 12.75 mmol/L, respectively), lowest ($P < 0.05$) for KAT sheep from the NW at 0800 h (10.02 mmol/L), and intermediate for the remaining sheep (Fig. 16). Likewise, no significant 2-way interactions were found for any of the blood characteristics evaluated except for a region × time interaction for plasma osmolality with sheep from the NW and SE having the highest ($P < 0.05$) and lowest ($P < 0.05$) values, respectively, at 0800 h, whereas the remaining sheep had intermediate values that were similar ($P > 0.05$). It was difficult, however, to draw clear trends from both interactions. As to the main effects, there were significant breed effects showing that STC had higher ($P < 0.05$) PCV (33.6 vs. 31.7%) and Hb concentration (12.60 vs. 12.02 g/dL) than DOR or KAT sheep which had similar ($P > 0.05$) values. There were also significant region effects showing that sheep from the NW had lower ($P < 0.05$) PCV (31.1 vs. 32.8%) and Hb concentration (11.75 vs. 12.36 g/dL) than sheep from the other regions which had similar ($P > 0.05$) values. Finally, the time of blood sampling had significant effects on Hb concentration and O_2 saturation with the former being higher ($P < 0.05$) at 0800 h and the latter being higher ($P < 0.05$) at 1400 h.

The *P* values for the main effects of and the interaction between breed and region as to the average values of serum metabolites in the last 2 wk of period 3 are presented in Table 18 with the corresponding means in Table 19. No significant breed × region interactions were found for any of the metabolites evaluated except for creatinine concentration that was highest ($P < 0.05$) for DOR from the NW, lowest ($P < 0.05$) for STC from the NW and SE, and intermediate for the remaining sheep. As to the main effects, glucose was the only metabolite significantly affected by breed with STC sheep having a higher ($P < 0.05$) concentration than those for DOR or KAT sheep (59.2 vs. 54.0 mg/dL) which were similar ($P > 0.05$). These glucose concentrations were within the normal range (30.4-64.3 mg/dL) for sheep (Hindson and Winter, 1996; Martin and Aitken, 2000; Cork and Halliwell, 2002). As to the region, it had no effects on any of the serum metabolites measured except cholesterol concentration that was highest ($P < 0.05$) for sheep from the MW, lowest ($P < 0.05$) for those from the NW, and intermediate for those from the SE and TX. The average serum cholesterol concentration for all groups were within the normal range (38.7-100.5 mg/dL) established for sheep (Martin and Aitken, 2000). Notably, creatinine concentration across regions was lowest ($P < 0.05$) for STC than DOR or KAT sheep, which had similar ($P > 0.05$) values (0.838 vs. 0.917 mg/dL).

Spearman Ranking and Variance

Spearman rank correlation coefficients (*sr*) among the 3 experimental periods and also among the 5 wk of period 3 when the sheep were offered water at 50% of ad libitum intake for plasma osmolality, PCV, and Hb concentration are in Tables 20, 21, and 22, respectively, whereas the *P* values for Bartlett's homogeneity of variance tests of those variables are in Table 22. In Table 20, the *sr* values between periods for plasma osmolality of the sheep breeds were significant for most comparisons and ranged between 0.28 and 0.50, 0.24 and 0.29, 0.28 and 0.50, and 0.17 and 0.42 for DOR, KAT, STC, and overall, respectively. The overall *sr* values, however, were low because many *sr* values were not significant between certain periods for KAT and STC sheep. For example, the rankings for plasma osmolality between periods 1 and 2 at 1400 h had no correlation for KAT (P = 0.263) or STC (P = 0.193) sheep. Similarly, neither KAT nor STC sheep had significant *sr* values between periods 1 and 3 at 0800 h ($P \geq 0.258$) or 1400 h ($P \geq 0.064$). The *sr* values between periods 2 and 3, however, were significant for all breeds except KAT at 0800 h (P = 0.281). When both times of blood sampling were considered, the *sr* ranked period 2-3 > 1-2 > 1-3 for KAT and STC sheep and for overall. In contrast, the *sr* values for DOR sheep were fairly similar for all comparisons. The comparisons for plasma osmolality among the 5 wk of period 3 (Table 20) showed that the *sr* values for the 10 comparisons made for each sheep breed were not significant at 0800 h except for wk 3-4 for DOR, wk 2-4, 3-4, and 4-5 for KAT, and wk 1-5 and 3-4 for STC. The same comparisons were significant at 1400 h except for wk 1-3, 1-4, 1-5, and 3-5 for KAT and wk 1-4, 2-4, and 3-4 for STC. Notably, the significance of the *sr* values for the overall and the average for both times of blood sampling were attributable to the significant *sr* values for certain breed comparisons at 0800 h and most comparisons at 1400 h. It is also worth noting that all *sr* values were significant for all breeds and overall at both times of blood sampling only once and that was for the wk 2-3 comparison. As to the significant *sr* values for the 10 comparisons made for DOR, KAT, and STC sheep and overall, they ranged between 0.32 and 0.61, 0.35 and 0.69, 0.31 and 0.61, and 0.22 and 0.55, respectively. Generally, there was no particular breed for which *sr* was consistently greater than other breeds in the comparisons made at either time of blood sampling and when both times were considered, the *sr* values were difficult to rank.

In Table 21, the *sr* values between periods for PCV of the sheep breeds were significant for all comparisons except for STC between periods 1 and 3 at 1400 h (P = 0.054) and ranged between 0.40 and 0.69, 0.48 and 0.76, 0.43 and 0.70, and 0.38 and 0.70 for DOR, KAT, STC, and overall, respectively. The *sr* values were greater for all breeds and overall at 0800 h than at 1400 h except for DOR between periods 1 and 2 and for KAT between periods 1 and 3 and periods 2 and 3. When both times of blood sampling were considered, the *sr* ranked period 1-2 > 2-3 > 1-3 for DOR and STC sheep and for overall. For KAT sheep, however, the *sr* ranked period 1-2 > 2-3 > 1-3. The comparisons for PCV among the 5 wk of period 3 (Table 21) showed that the *sr* values for the 10 comparisons for each breed were significant at both times of blood sampling except for STC at 0800 h of the wk 1-3 comparison. As to the significant *sr* values for the 10 comparisons made for DOR, KAT, and STC sheep and overall, they ranged between 0.51 and 0.86, 0.39 and 0.78, 0.38 and 0.67, and 0.45 and 0.76, respectively. With few exceptions, DOR sheep consistently had greater *sr* values than KAT or STC sheep at either time of blood sampling and when both times were considered in the average values presented. Interestingly, DOR sheep had the same average values for overall in all the comparisons except for wk 1-2. The *sr* values, however, were difficult to rank.

In Table 22, the *sr* values between periods for Hb concentration in the sheep breeds displayed patterns resembling those described for PCV (Table 21), were significant for all comparisons and ranged between 0.61 and 0.72, 0.50 and 0.86, 0.39

and 0.78, and 0.54 and 0.75 for DOR, KAT, STC, and overall, respectively. In general, the *sr* values were greater at 0800 h than at 1400 h except for DOR between periods 1 and 2, for KAT between periods 1 and 3 and periods 2 and 3, for STC between periods 2 and 3, and for overall between periods 1 and 3. When both times of blood sampling were considered, the *sr* ranked period 1-2 > 2-3 > 1-3 for DOR and STC sheep and for overall. For KAT sheep, however, the *sr* ranked period 1-2 > 2-3 > 1-3. The comparisons for Hb concentration among the 5 wk of period 3 (Table 22) showed that the *sr* values for the 10 comparisons for each breed were significant at both times of blood sampling and ranged between 0.60 and 0.90, 0.33 and 0.82, 0.48 and 0.81, and 0.55 and 0.81 for DOR, KAT, and STC sheep and overall, respectively. With few exceptions, DOR sheep consistently had greater *sr* values than KAT or STC sheep at either time of blood sampling and when both times were considered in the average values presented. The *sr* values, however, were difficult to rank.

The fact that all spearman rank correlation coefficients among periods were different from 0 for DOR sheep suggests that the plasma osmolality rankings observed in period 1 can reasonably predict the rankings in periods 2 and 3. However, the same generalization cannot be made for KAT or STC sheep, particularly when baseline conditions (period 1) were compared with the most severe water restriction level (period 3). It was clear that the rankings were affected by time of blood sampling (0800 vs. 1400 h) which may have reflected differences in the dehydration status because water offered to the sheep at 0730 h, minutes before the morning sampling. Spearman rank correlation coefficients among the 5 wk of period 3 revealed that the rankings were most likely consistent when the weeks being compared are adjacent to each other such as wk 1 and 2.

Spearman rank correlation coefficients for PCV indicated that the rankings observed in period 1 can accurately predict the rankings in the periods of water restriction. The same conclusion can be made for the comparisons among the 5 wk of period 3. Unlike osmolality, the PCV results suggest that the rankings in wk 1 also represent the rankings in subsequent weeks. For Hb concentration, it was not surprising that ranking correlations were similar to that of PCV because Hb is a component of red blood cells and PCV is a measure of red blood cells as a proportion whole blood.

Homogeneity of variance tests for plasma osmolality, PCV, and Hb concentration during the last 2 wk of period 3 (Table 23) showed that restricting WI to 50% of ad libitum can have different effects on the 3 breeds evaluated as shown in the heterogeneous variance among breeds for each of those blood characteristics. At each sampling time, the variance for osmolality, PCV, and Hb concentration was smaller for STC than for DOR or KAT sheep, whereas the variance for osmolality was larger for KAT than for DOR sheep. The lower variability in plasma osmolality, PCV, and Hb concentration at 0800 h is difficult to interpret in regard to resilience. The larger variance for osmolality and PCV measurements in KAT sheep is also difficult to interpret considering that sample size was slightly larger for KAT than for DOR and STC sheep. As to the other response variables (i.e., O_2 saturation and O_2 concentration), however, the variance, was homogenous ($P \geq 0.148$) among breeds.

Physiological Responses of Small Ruminants to Water Shortage

In previous water restriction studies, understanding the physiological mechanisms behind resilience of adapted small ruminants to limited water availability was achieved by monitoring blood characteristics and metabolites sensitive to drinking water shortage.

In each of those studies, a few of the blood indictors evaluated in the present study were reported.

Comparing intermittent watering regimes to watering daily, dry Awassi ewes were offered water every 3 d for 23 d (Hamadeh et al., 2006) or every 4 d for 42 d (Jaber et al., 2004), 24 d (Jaber et al., 2001), and 12 d (Ghanem et al., 2008). In the study of Hamadeh et al. (2006), water restriction increased serum concentrations of albumin (3.43 vs. 3.08 g/dL), cholesterol (92.8 vs. 65.7 mg/dL), creatinine (1.092 vs. 0.941 mg/dL), total protein (7.86 vs. 7.39 g/dL), and urea (60.1 vs. 49.8 mg/dL), but did not affect PCV or concentrations of Hb and serum glucose (averaging 30.1%, 11.5 g/dL, and 35.6 mg/dL, respectively). Jaber et al. (2004) also reported that water restriction increased serum concentrations of cholesterol (82.7 vs. 75.4 mg/dL), creatinine (1.135 vs. 0.957 mg/dL), total protein (8.03 vs. 7.59 g/dL), and urea (46.3 vs. 35.8 mg/dL), decreased albumin concentration (2.98 vs. 3.11 g/dL), but did not affect PCV or concentrations of Hb and serum glucose (averaging 28.6%, 10.9 g/dL, and 49.9 mg/dL, respectively). Jaber et al. (2011) later reported that serum cholesterol concentration increased with water restriction (69.9 vs. 46.4 mg/dL). In the study of Ghanem et al. (2008), however, water restriction increased PCV (35.9 vs. 29.9%) and Hb concentration (15.5 vs. 13.6 g/dL). It also increased serum concentrations of albumin (4.22 vs. 3.47 g/dL), cholesterol (79.6 vs. 62.2 mg/dL), and total protein (9.80 vs. 7.95 g/dL), but did not alter glucose concentration (averaging 68.2 mg/dL).

In short-term studies, the sheep were given ad libitum access to water for days before depriving them of water for certain number of days (Laden et al., 1987; Igbokwe, 1993; Li et al., 2000). Depriving Awassi ewes of water for 5 d in a semiarid environment where temperatures varied between 14 to 20 °C at night and 36 to 41 °C during the day (Laden et al., 1987), increased plasma osmolality (328 vs. 278 mosm/L) and concentrations of creatinine and urea (1.5 vs. 0.8 and 111 vs. 44 mg/dL, respectively). Depriving Yankasa ewes of water for 5 d (Igbokwe, 1993) in another hot environment (up to 42 °C), however, did not affect PCV or plasma concentrations of albumin and total protein (averaging 27.3%, 4.94 g/dL, and 6.76 g/dL, respectively), but increased plasma concentrations of cholesterol, creatinine, and urea (92.8 vs. 61.9, 1.538 vs. 1.052, and 121.9 vs. 44.4 mg/dL, respectively). In contrast, less severe effect were reported by Li et al. (2000) as depriving male sheep (unidentified breed) of water for 3 d under controlled temperature (24.8 °C) increased Hb concentration (12.64 vs. 11.41 g/dL), but did not alter PCV or plasma volume, osmolality, and creatinine concentration (averaging 35.5%, 4.06 L, 291.7 mosm/L, and 0.840 mg/dL, respectively).

In other studies, the sheep were offered water daily at restricted amounts and were compared to others offered water ad libitum. For example, restricting WI by lactating Comisana ewes to 60% of ad libitum for 40 d (Casamassima et al., 2008) increased serum concentrations of albumin (3.48 vs. 3.25 g/dL), cholesterol (67.7 vs. 63.0 mg/dL), total protein (7.18 vs. 6.68 g/dL), and triglycerides (19.5 vs. 16.8 mg/dL), but did not affect concentrations of creatinine, glucose, or urea (averaging 1.091, 55.3, and 51.2 mg/dL, respectively). Casamassima et al. (2016) later reported that restricting WI by lactating Lacaune ewes to 60% of ad libitum for 28 d increased PCV (30.0 vs. 24.0%), Hb concentration (11.93 vs. 10.08 g/dL), and serum concentrations creatinine (1.196 vs. 1.038 mg/dL) and total protein (8.20 vs. 7.27 g/dL). However, Kumar et al. (2016) reported that restricting WI by nonpregnant Malpura ewes to 60% of ad libitum for 35 d did not affect PCV, Hb concentration, or plasma concentration of albumin (averaging 42.8%, 11.78 g/dL, and 3.55 g/dL, respectively), but decreased plasma concentrations of cholesterol (55.5 vs. 65.4 mg/dL) and glucose (46.3 vs. 51.2 mg/dL). In contrast, De et al. (2015) reported that restricting WI by nonpregnant Malpura ewes to 60% of ad libitum for 28 d increased PCV (47.4 vs. 34.9%), but did not affect Hb concentration (averaging 13.92 g/dL) or plasma concentrations of albumin and total protein (averaging 3.55 and 7.76 g/dL, respectively) as well as cholesterol and glucose (averaging 53.4 and 45.7 mg/dL, respectively). Restricting intake of water low or high in total dissolved solids by Baluchi lambs to 50% of ad libitum for 42 d (Vosooghi-Postindozet al., 2018) also did not affect Hb concentrations (averaging 10.53 g/dL) or serum concentrations of albumin and total protein (averaging 3.81 and 7.14 g/dL) as well as creatinine and glucose (averaging 1.065 and 65.5 mg/dL, respectively) across the water salinity treatments. Water restriction, however, increased PCV (28.5 vs. 26.2%) and concentrations of cholesterol and triglycerides (68.3 vs. 63.1 and 32.5 vs. 30.9 mg/dL, respectively). Giving Corriedale ewes access to water for only 2 h daily (Nejad et al., 2014), however, did not affect PCV, Hb concentration, or serum concentrations of glucose, total protein, or urea (averaging 29.0%, 8.9 g/dL, 51.5 mg/dL, 5.99 g/dL, and 58.2 mg/dL, respectively), but increased concentration of triglycerides (38.9 vs. 28.3 mg/dL). It is worth noting that in 3 studies cited above (Jaber et al., 2004; Hamadeh et al., 2006; Casamassima et al., 2016), creatinine concentrations were incorrectly listed in mmol/L, which made the reported levels physiologically impossible as they would have been about 500 times the maximum level in the normal range for creatinine concentration (i.e., 0.498 to 1.923 mg/dL) in sheep (Hindson and Winter, 1996; Martin and Aitken, 2000; Cork and Halliwell, 2002).

Thus, those concentrations were assumed to have been in μmol/L for the above listed comparisons.

Research with goats demonstrated that depriving Hipsi, Aardi, and Zumri bucks of water for 3 d (Alamer, 2006), steadily increased PCV from 29.3 to 38.4% and plasma osmolality from 289.3 to 337.3 mosm/L across breeds at the end of the 3-d period. Offering lactating Ethiopian Somali does water every 4 d versus every day for 32 d, Mengistu et al. (2007a) showed that such an intermittent watering regime increased plasma osmolality and total protein concentration at the end of the 4-d water deprivation periods (averaging 312.5 vs. 305.0 mosm/L and 8.18 vs. 7.90 g/dL, respectively). Offering Ethiopian Somali bucks water every 4 d for 72 d, Mengistu et al. (2007b) also showed increased plasma osmolality and total protein concentration at the end of the 4-d water deprivation periods (averaging 314.0 vs. 304.0 mosm/L and 6.80 vs. 6.65 g/dL, respectively). Depriving dry Nubian does of water for 3 d (Abdelatif et al., 2010) was also shown to increase PCV (37.0 vs. 25.8%), serum osmolality (344.0 vs. 276.5 mosm/L), and serum concentrations of albumin and total protein (4.3 vs. 3.0 and 8.9 vs. 7.1 g/dL, respectively) as well as creatinine and urea (1.10 vs. 0.68 and 40.5 vs. 29.8 mg/dL, respectively). Serum glucose concentration, however, was not affected by dehydration (averaging 68.9 mg/dL). Restricting daily WI of Tswana and Boer goat wethers to 50% of ad libitum for 7 d increased PCV (27.8 vs. 25.8%), plasma osmolality (330.8 vs. 315.8 mosm/L), and plasma concentrations of total protein (7.31 vs. 6.58 g/dL) and urea (54.1 vs. 43.2 mg/dL) across breeds (Qinisa et al., 2011). In another study (Kaliber et al., 2016) plasma concentrations of cholesterol (47, 51, 54, and 62 mg/dL), creatinine (0.31, 0.35, 0.39, and 0.43 mg/dL), glucose (57, 62, 67, and 70 mg/dL), and urea (48, 50, 51, and 55 mg/dL) increased in a manner reflecting restriction of daily WI by crossbred German Fawn does from 100 to 87, 73, and 56% of ad libitum, respectively.

The variable physiological responses among these studies is evident in that water restriction did not affect many of the blood measurement evaluated, decreased albumin by 4.2% (Jaber et al., 2004) and both cholesterol and glucose by 15.1 and 9.6%, respectively (Kumar et al., 2016), and increased one or more measurements in each study. The magnitude of those increases however, varied for blood PCV (2.0 to 12.5 percentage units) and Hb concentration (14.0 to 18.4%), serum or plasma osmolality (10.0 to 67.5 mosm/L), and serum or plasma concentrations of albumin (8.6 to 43.3%), cholesterol (7.5 to 50.6%), creatinine (15.2 to 98.9%), glucose (22.8%), total protein (2.3 to 25.4%), triglycerides (5.2 to 37.5%), and urea (14.6 to 174.5%). Aside from the differences in genetic potential to cope with drinking water shortage among the various breeds of sheep or goats evaluated, the reported responses were more likely affected by other factors, including heat stress, nutritional and physiological state, severity of the water-restriction treatment, and/or the experimental design used, especially the very small number of animals used in many studies. As a result, it is difficult to make meaningful comparisons between the results of the present study and many of the above mentioned studies.

Resilience of the Three Hair Sheep Breeds to Severe Water Shortage

Except for one study in which KAT sheep were compared to 2 breeds of goats (Mengistu et al., 2016), no studies have been found evaluating resilience of hair sheep breeds to drinking water shortage. This was due to the fact that previous studies focused on establishing how other sheep breeds (Aganga et al., 1989; Hamadeh et al., 2006; De et al., 2015) and some goat breeds (Alamer, 2006; Mengistu et al., 2007a; Kaliber et al., 2016) native to arid (e.g., Ethiopia, India, Nigeria, and Saudi Arabia) and semiarid (e.g., Lebanon and Israel) environments cope with drought conditions.

The results of the present study suggest that the 3 hair sheep breeds were equally resilient to 50% water restriction. Moreover, across the 3 hair sheep breeds, 4 climatic regions, and 2 times of blood sampling, such a severe water restriction resulted in minor increases over baseline (ad libitum WI) values for PCV (32.4 vs. 31.6%), Hb concentration (12.35 vs. 11.95 g/dL), plasma osmolality (308.5 vs. 301.5 mosm/L), and both O_2 saturation (69.4 vs. 67.1%) and concentration (11.51 vs. 10.65 mmol/L). These responses reflected the sheep ability to maintain plasma volume by decreasing water losses and efficient use of the rumen as a water reservoir to replenish any losses in plasma volume (Silanikove, 1994). As to the serum metabolites measured, water restriction increased concentrations of albumin (2.68 vs. 2.59 g/dL), cholesterol (70.5 vs. 56.4 mg/dL), creatinine (0.972 vs. 0.840 mg/dL), glucose (59.8 vs. 55.6 mg/dL), triglycerides (35.1 vs. 28.8 mg/dL), and urea (22.4 vs. 19.4 mg/dL) by 3.5, 25.0, 15.7, 7.6, 21.9, and 15.5%, respectively. The increases in concentrations of creatinine and urea, respectively, underscore the kidney role in water conservation through slower glomerular filtration and higher urea reabsorption (Kataria and Kataria, 2007). The serum concentration of urea was also within the normal range (17.5-48.2 mg/dL) for sheep (Hindson and Winter, 1996; Martin and Aitken, 2000; Cork and Halliwell, 2002). Importantly, the increases in concentrations of albumin and glucose combined with that concentrations of lactate and total protein were not altered by water restriction (averaging 23.2 mg/dL and 7.18 g/dL, respectively) demonstrate that the sheep ability to meet their requirements of amino acids and glucose was not compromised. The serum concentration of lactate was within the normal range (9.1-27.0 mg/dL) established for sheep by Martin and Aitken (2000). Serum total protein concentration was also within physiological norms (6-8 g/dL) for sheep (Hindson and Winter, 1996; Martin and Aitken, 2000; Cork and Halliwell, 2002). However, the increases in concentrations of cholesterol and triglycerides reflect mobilization of body fat to support additional energy needs for activated metabolic functions to cope with the stress of severe shortage in drinking water and to produce metabolic water.

CONCLUSION

Using measurements of blood characteristics and serum metabolites sensitive to drinking water shortage, resilience of 3 hair sheep breeds from 4 climatic regions to limited water availability was examined at 50% of ad libitum WI for 5 wk following a baseline and intermediate water restriction period of 2 wk each in which the sheep were offered 100 and 75% of ad libitum WI, respectively. Across breeds and regions, all sheep exhibited different but minor changes in blood characteristics and serum metabolites while under 75% water restriction, needed 1 wk in period 3 to adapt to the most severe restriction treatment, and maintained levels of those measurements that were slightly higher than baseline values thereafter. The results suggested that the 3 hair sheep breeds had high resilience to limited water availability in the absence of heat stress.

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Table 1. Temperature, relative humidity (RH), heat load index (HLI), and temperature-humidity index (THI) (mean ± SEM) outside and inside the room where the hair sheep were housed during 4 trials[1]

Location[2]	Period	Time[3]	Temperature, ºC	RH, %	HLI	THI
Outside	1	Day	18.3 ± 7.31	56.9 ± 2.80	69.7 ± 11.32	43.3 ± 10.11
		Night	13.6 ± 6.71	74.5 ± 3.43	69.0 ± 11.54	45.4 ± 11.76
	2	Day	21.3 ± 6.00	51.5 ± 3.93	72.2 ± 9.73	44.6 ± 8.60
		Night	16.1 ± 5.78	70.3 ± 3.63	71.3 ± 9.77	47.0 ± 9.76
	3	Day	21.1 ± 4.32	54.6 ± 3.46	73.2 ± 7.85	46.3 ± 7.44
		Night	15.9 ± 4.17	73.6 ± 4.88	72.3 ± 8.18	48.5 ± 8.57
Inside	1	Day	23.4 ± 3.38	48.3 ± 5.05	74.3 ± 8.71	45.8 ± 10.82
		Night	22.9 ± 3.29	49.6 ± 4.08	74.0 ± 8.40	45.9 ± 10.25
	2	Day	19.7 ± 5.64	58.3 ± 3.73	72.3 ± 10.08	46.3 ± 9.78
		Night	18.8 ± 6.45	59.7 ± 1.99	71.4 ± 10.28	45.4 ± 9.53
	3	Day	18.8 ± 4.10	60.8 ± 5.75	71.9 ± 8.51	46.4 ± 8.81
		Night	17.6 ± 4.77	61.8 ± 4.08	70.4 ± 8.61	45.1 ± 8.55

[1] The sheep were offered water ad libitum intake for 2 wk (period 1), 75% of ad libitum intake for 2 wk (period 2), and 50% of ad libitum intake for 5 wk (period 3).
[2]Outside data were averages for 4 trials and inside data were averages for 3 trials.
[3]Daytime was from 0700 h to 1900 h and nighttime was from 1900 h to 0700 h.

Table 2. Ingredient and nutrient composition of diet fed to hair sheep

Item	Concentration
Ingredient, % as fed basis	
Cottonseed hulls	29.06
Ground corn	19.98
Dehydrated alfalfa	19.98
Wheat middlings	13.00
Cottonseed meal	8.99
Pelleting agent	4.99
Salt	1.00
Calcium carbonate	0.95
Ammonium chloride	1.00
Yeast	1.00
Vitamin-mineral mix[1]	0.05
Rumensin 90 premix[2]	0.01
Nutrient composition, dry matter basis[3]	
Ash, %	8.7 ± 0.43
Crude protein, %	18.6 ± 0.46
Neutral detergent fiber, %	37.7 ± 0.95
Gross energy, MJ/kg	16.9 ± 0.12

[1]Composition: 1.28% Zn; 0.96% Fe; 0.704% Mn; 0.16% Cu; 0.048% I; 0.032% Co; 26,460,000 IU/kg vitamin A; 6,615,000 IU/kg vitamin D_3, and 11,025 IU/kg vitamin E.
[2]Supplied 20% monensin.
[3]Analysis of weekly composite samples formed from daily samples.

Table 3. *P* values for effects of breed (B), region (R), time of blood sampling (T), animal set, and initial age on blood characteristics of hair sheep offered water ad libitum for 2 wk (period 1)

	Variable[1]				
Source of variation[2]	Osmolality, mosm/L	PCV, %	Hb concentration, g/dL	O_2 saturation, %	O_2 concentration, mmol/L
B	0.001	0.569	0.616	0.135	0.283
R	0.565	0.293	0.287	0.243	0.247
T	<0.001	<0.001	<0.001	<0.001	<0.001
B*R	0.638	0.488	0.611	0.078	0.063
B*T	0.866	0.363	0.650	0.928	0.683
R*T	0.806	0.729	0.162	0.053	0.159
B*R*T	0.937	0.677	0.152	0.358	0.248
Set	<0.001	0.164	0.077	0.001	0.007
Age	0.709	0.539	0.416	0.156	0.054

[1] PCV = packed cell volume; Hb = hemoglobin; O_2 = oxygen.

[2]In each of 4 separate trials (9 wk each), a different set of sheep of 3 breeds (Dorper, Katahdin, and St. Croix) with each representing 4 U.S. climatic regions (the Midwest, Northwest, Southeast, and Central Texas) was used and blood samples were collected twice weekly (Wednesday at 0800 h and Thursday at 1400 h).

Table 4. Effects of breed, region, and time of blood sampling on blood characteristics of hair sheep offered water ad libitum for 2 wk (period 1)

	Breed[1]				Region[2]					Time, h		
Variable[3]	DOR	KAT	STC	SEM	MW	NW	SE	TX	SEM	0800	1400	SEM
Osmolality, mosm/L	300.1[b]	302.1[a]	302.6[a]	0.52	301.6	301.2	301.3	302.3	0.60	300.2[b]	303.0[a]	0.38
PCV, %	31.9	31.3	31.9	0.48	32.5	31.6	31.0	31.6	0.55	32.3[a]	31.1[b]	0.28
Hb concentration, g/dL	12.09	11.91	11.85	0.179	12.28	11.85	11.74	11.91	0.207	12.09[a]	11.80[b]	0.104
O_2 saturation, %	63.9	65.4	68.4	1.56	66.0	68.9	64.6	64.1	1.80	68.9[a]	62.9[b]	1.11
O_2 concentration, mmol/L	10.44	10.50	11.00	0.268	10.87	11.03	10.25	10.43	0.309	11.22[a]	10.07[b]	0.180

[1] DOR = Dorper; KAT = Katahdin; STC = St. Croix.
[2] MW = Midwest; NW = Northwest; SE = Southeast; TX = Central Texas.
[3] PCV = packed cell volume; Hb = hemoglobin; O_2 = oxygen.
[a,b]Main effect means without a common superscript letter differ (P < 0.05).

Table 5. *P* values for effects of breed (B), region (R), animal set, and initial age on serum metabolites of hair sheep offered water ad libitum for 2 wk (period 1)

	Variable							
Source of variation[1]	Albumin, g/dL	Cholesterol, mg/dL	Creatinine, mg/dL	Glucose, mg/dL	Lactate, mg/dL	Total protein, g/dL	Triglycerides, mg/dL	Urea, mg/dL
B	0.778	0.012	0.091	0.607	0.126	0.365	0.027	0.255
R	0.654	0.781	0.906	0.209	0.503	0.662	0.527	0.807
B*R	0.237	0.186	0.335	0.801	0.168	0.538	0.432	0.240
Set	0.002	<0.001	0.101	<0.001	<0.001	0.308	<0.001	0.381
Age	0.430	0.342	0.696	0.277	0.832	0.009	0.092	0.475

[1]In each of 4 separate trials (9 wk each), a different set of sheep of 3 breeds (Dorper, Katahdin, and St. Croix) with each representing 4 U.S. climatic regions (the Midwest, Northwest, Southeast, and Central Texas) was used.

Table 6. Effects of breed and region on serum metabolites of hair sheep offered water ad libitum for 2 wk (period 1)

	Breed[1]				Region[2]				
Variable	DOR	KAT	STC	SEM	MW	NW	SE	TX	SEM
Albumin, g/dL	2.46	2.59	2.51	0.142	2.48	2.39	2.53	2.67	0.162
Cholesterol, mg/dL	42.9[b]	67.1[a]	57.2[ab]	6.34	51.3	54.6	56.1	60.9	7.06
Creatinine, mg/dL	0.851	0.762	0.695	0.054	0.758	0.765	0.748	0.807	0.062
Glucose, mg/dL	55.2	53.4	58.1	3.58	59.3	48.9	54.6	59.4	4.12
Lactate, mg/dL	19.4	29.0	26.1	3.58	24.6	29.7	23.5	21.5	4.04
Total protein, g/dL	6.78	6.99	7.28	0.252	6.74	6.98	7.22	7.12	0.291
Triglycerides, mg/dL	24.2[b]	36.8[a]	25.7[b]	3.77	25.6	33.6	26.5	29.8	4.31
Urea, mg/dL	35.7	40.4	43.0	3.36	39.4	37.2	42.2	40.0	3.81

[1] DOR = Dorper; KAT = Katahdin; STC = St. Croix.
[2] MW = Midwest; NW = Northwest; SE = Southeast; TX = Central Texas.
[a,b]Main effect means without a common superscript letter differ ($P < 0.05$).

Table 7. *P* values for effects of breed (B), region (R), period (P), week within period (W), time of blood sampling (T), animal set, and initial age on blood characteristics of hair sheep[1]

	Variable[2]				
Source of variation[3]	Osmolality, mosm/L	PCV, %	Hb concentration, g/dL	O_2 saturation, %	O_2 concentration, mmol/L
B	0.042	0.194	0.497	0.001	0.002
R	0.640	0.355	0.394	0.726	0.907
P	<0.001	<0.001	0.584	0.008	<0.001
W	0.004	0.041	0.717	0.402	0.498
T	<0.001	<0.001	0.004	0.005	<0.001
B*R	0.628	0.382	0.561	0.517	0.248
B*P	0.020	<0.001	0.085	0.471	0.402
B*W	0.129	0.120	0.736	0.459	0.567
B*T	0.886	0.310	0.703	0.587	0.336
R*P	0.019	0.005	0.986	0.284	0.063
R*W	0.082	0.722	0.228	0.516	0.212
R*T	0.591	0.591	0.454	0.342	0.658
P*W	<0.001	0.118	0.364	0.074	0.058
P*T	0.862	0.327	0.424	0.027	0.084
W*T	0.049	0.305	0.447	0.701	0.972
B*R*P	0.276	0.005	0.738	0.004	0.070
B*R*W	0.075	0.507	0.374	0.596	0.700
B*R*T	0.939	0.821	0.663	0.456	0.383
B*P*W	0.202	0.393	0.754	0.738	0.394
B*P*T	0.779	0.991	0.460	0.283	0.477
B*W*T	0.982	0.855	0.465	0.596	0.469
R*P*W	0.231	0.518	0.264	0.829	0.508
R*P*T	0.875	0.447	0.690	0.126	0.285
R*W*T	0.213	0.583	0.394	0.674	0.921
P*W*T	0.003	0.026	0.405	0.041	0.262
B*R*P*W	0.939	0.199	0.606	0.159	0.128

B*R*P*T	0.828	0.802	0.741	0.146	0.203
B*R*W*T	0.693	0.937	0.706	0.193	0.209
B*P*W*T	0.701	0.825	0.578	0.865	0.856
R*P*W*T	0.945	0.862	0.605	0.469	0.657
B*R*P*W*T	0.525	0.995	0.708	0.798	0.974
Set	<0.001	0.672	0.975	<0.001	<0.001
Age	0.828	0.528	0.296	0.140	0.129

[1] The sheep were offered water ad libitum for 2 wk in period 1, 75% of ad libitum intake for 2 wk in period 2, and 50% of ad libitum intake for 2 wk of period 3.

[2] PCV = packed cell volume; Hb = hemoglobin; O_2 = oxygen.

[3]In each of 4 separate trials (9 wk each), a different set of sheep of 3 breeds (Dorper, Katahdin, and St. Croix) with each representing 4 U.S. climatic regions (the Midwest, Northwest, Southeast, and Central Texas) was used and blood samples were collected twice weekly (Wednesday at 0800 h and Thursday at 1400 h).

Table 8. Effects of breed and period on blood characteristics of hair sheep

		Breed[1]				Period[2]			
Variable[3]	Breed	DOR	KAT	STC	SEM	1	2	3	SEM
PCV, %	DOR					32.1^{abc}	31.6^{bc}	31.9^{abc}	0.49
	KAT					30.7^{c}	31.3^{c}	32.0^{abc}	
	STC					31.8^{bc}	32.7^{ab}	33.2^{a}	
Hb concentration, g/dL		12.24	11.90	12.21	0.222				
O_2 saturation, %		66.2^{b}	65.6^{b}	71.9^{a}	1.22				
O_2 concentration, mmol/L		10.77^{b}	10.52^{b}	11.77^{a}	0.247				

[1]DOR = Dorper; KAT = Katahdin; STC = St. Croix.

[2]The sheep were offered water ad libitum for 2 wk in period 1, 75% of ad libitum intake for 2 wk in period 2, and 50% of ad libitum intake for 2 wk of period 3.

[3] PCV = packed cell volume; Hb = hemoglobin; O_2 = oxygen.

[a,b]Main effect means within a row without a common superscript letter differ ($P < 0.05$); presence of interaction means denotes a significant interaction ($P < 0.05$); [a,b,c]interaction means without a common superscript letter differ ($P < 0.05$).

Table 9. *P* values for effects of breed (B), region (R), period (P), animal set, and initial age on serum metabolites of hair sheep[1]

	Variable							
Source of variation[2]	Albumin, g/dL	Cholesterol, mg/dL	Creatinine, mg/dL	Glucose, mg/dL	Lactate, mg/dL	Total protein, g/dL	Triglycerides, mg/dL	Urea, mg/dL
B	0.589	0.058	<0.001	0.092	0.548	0.603	0.001	0.067
R	0.609	0.728	0.569	0.938	0.236	0.299	0.679	0.133
P	<0.001	<0.001	<0.001	<0.001	0.088	<0.001	<0.001	<0.001
B*R	0.032	0.246	0.020	0.151	0.745	0.087	0.099	0.289
B*P	0.541	0.623	0.287	0.608	0.396	0.673	0.923	0.830
R*P	0.920	0.373	0.614	0.947	0.497	0.940	0.751	0.920
B*R*P	0.608	0.201	0.351	0.086	0.610	0.149	0.748	0.163
Set	<0.001	<0.001	0.017	<0.001	<0.001	<0.001	<0.001	<0.001
Age	0.045	0.628	0.284	0.070	0.109	0.060	0.329	0.623

[1]The sheep were offered water ad libitum for 2 wk in period 1, 75% of ad libitum intake for 2 wk in period 2, and 50% of ad libitum intake for 2 wk of period 3.

[2] In each of 4 separate trials (9 wk each), a different set of sheep of 3 breeds (Dorper, Katahdin, and St. Croix) with each representing 4 U.S. climatic regions (the Midwest, Northwest, Southeast, and Central Texas) was used.

Table 10. Effects of breed, region, and period on serum metabolites of hair sheep

		Breed[1]				Region[2]					Period[3]			
Variable	Breed	DOR	KAT	STC	SEM	MW	NW	SE	TX	SEM	1	2	3	SEM
Albumin, g/dL		2.57	2.58	2.54	0.029						2.59^{b}	2.43^{c}	2.68^{a}	0.027
	DOR					2.65^{a}	2.60^{ab}	2.54^{ab}	2.50^{ab}	0.059				
	KAT					2.57^{ab}	2.66^{a}	2.64^{a}	2.46^{b}					
	STC					2.45^{b}	2.51^{ab}	2.57^{ab}	2.64^{a}					
Cholesterol, mg/dL		60.5	64.9	59.0	1.74	63.1	60.3	60.4	62.1	1.99	56.4^{b}	57.4^{b}	70.5^{a}	1.25
Creatinine, mg/dL		0.978^{a}	0.872^{b}	0.778^{c}	0.016						0.840^{b}	0.816^{b}	0.972^{a}	0.013
	DOR					1.003^{ab}	1.049^{a}	0.927^{bcd}	0.935^{bc}	0.032				
	KAT					0.842^{de}	0.896^{cd}	0.914^{cd}	0.837^{de}					
	STC					0.769^{ef}	0.740^{f}	0.796^{ef}	0.805^{ef}					
Glucose, mg/dL		53.5	55.5	56.7	1.03	54.6	55.5	55.5	55.5	1.19	55.6^{b}	50.4^{c}	59.8^{a}	0.99
Lactate, mg/dL		21.9	22.7	23.3	0.87	23.3	24.0	21.7	21.5	1.01	24.0	21.4	22.4	0.83
Total protein, g/dL		6.95	6.96	7.07	0.097	6.92	7.09	7.10	6.85	0.113	7.08^{a}	6.62^{b}	7.28^{a}	0.081
Triglycerides, mg/dL		30.4^{b}	34.8^{a}	27.7^{b}	1.33	30.3	32.5	31.1	30.0	1.55	28.8^{b}	28.9^{b}	35.1^{a}	1.0
Urea, mg/dL		43.7	43.9	46.7	1.03	44.9	44.7	46.4	42.6	1.18	41.5^{c}	44.5^{b}	47.9^{a}	0.79

[1]DOR = Dorper; KAT = Katahdin; STC = St. Croix.

[2]MW = Midwest; NW = Northwest; SE = Southeast; TX = Central Texas.

[3]The sheep were offered water ad libitum for 2 wk in period 1, 75% of ad libitum intake for 2 wk in period 2, and 50% of ad libitum intake for 2 wk of period 3.

[a,b,c] [b]Main effect means within a row without a common superscript letter differ (*P* < 0.05); presence of interaction means denotes a significant interaction (*P* < 0.05); [a,b,c,d,e,f]interaction means without a common superscript letter differ (*P* < 0.05).

Table 11. *P* values for effects of breed (B), region (R), week (W), time of blood sampling (T), animal set, and initial age on blood characteristics of hair sheep offered water at 50% of ad libitum intake for 5 wk (period 3)

	Variable[1]				
Source of variation[2]	Osmolality, mosm/L	PCV, %	Hb concentration, g/dL	O_2 saturation, %	O_2 concentration, mmol/L
B	0.071	0.006	0.310	0.001	<0.001
R	0.755	0.006	0.016	0.490	0.091
W	<0.001	0.070	0.006	0.001	0.075
T	<0.001	<0.001	<0.001	0.002	0.712
B*R	0.408	0.072	0.071	0.282	0.286
B*W	0.769	0.024	0.001	0.049	0.294
B*T	0.174	0.381	0.087	0.448	0.521
R*W	0.004	0.178	0.493	0.186	0.100
R*T	0.028	0.287	0.607	0.024	0.086
W*T	<0.001	<0.001	0.019	0.014	0.417
B*R*W	0.715	<0.001	<0.001	0.141	0.175
B*R*T	0.975	0.722	0.858	0.354	0.369
B*W*T	0.799	0.390	0.255	0.716	0.969
R*W*T	0.886	0.851	0.993	0.186	0.454
B*R*W*T	0.447	0.855	0.954	0.188	0.245
Set	<0.001	0.006	0.002	<0.001	<0.001
Age	0.714	0.982	0.844	0.111	0.129
Covariate	0.365	<0.001	0.089	<0.001	<0.001

[1] PCV = packed cell volume; Hb = hemoglobin; O_2 = oxygen.

[2]In each of 4 separate trials (9 wk each), a different set of sheep of 3 breeds (Dorper, Katahdin, and St. Croix) with each representing 4 U.S. climatic regions (the Midwest, Northwest, Southeast, and Central Texas) was used and blood samples were collected twice weekly (Wednesday at 0800 h and Thursday at 1400 h).

Table 12. Effects of breed and week on blood characteristics of hair sheep offered water at 50% of ad libitum intake for 5 wk (period 3)

		Breed[1]				Week					
Variable[2]	Breed	DOR	KAT	STC	SEM	1	2	3	4	5	SEM
Osmolality, mosm/L		306.8	308.3	306.3	0.62	311.4[a]	306.3[bc]	305.7[bc]	305.5[c]	306.8[b]	0.53
PCV, %	DOR					32.2[cdef]	31.8[ef]	32.1[def]	31.5[ef]	31.7[ef]	0.42
	KAT					33.0[abcd]	32.3[bcde]	32.5[bcde]	32.0[def]	31.5[f]	
	STC					33.3[abc]	33.1[abcd]	33.4[abc]	33.5[ab]	33.8[a]	
Hb concentration, g/dL	DOR					12.31[ab]	12.09[ab]	12.15[ab]	11.96[b]	12.18[ab]	0.175
	KAT					12.54[a]	12.31[ab]	12.36[ab]	12.08[ab]	11.91[b]	
	STC					12.53[a]	12.34[ab]	12.37[ab]	12.53[a]	12.59[a]	
O_2 saturation, %	DOR					66.6[de]	70.0[cd]	68.9[cde]	72.4[abc]	67.1[de]	1.49
	KAT					65.0[e]	68.7[cde]	67.8[de]	71.3[bc]	67.6[de]	
	STC					72.3[bc]	74.5[ab]	76.3[a]	72.6[abc]	74.2[ab]	
O_2 concentration, mmol/L		11.19[b]	11.15[b]	12.32[a]	0.195	11.39	11.62	11.58	11.78	11.40	0.147

[1] DOR = Dorper; KAT = Katahdin; STC = St. Croix.

[2] PCV = packed cell volume; Hb = hemoglobin; O_2 = oxygen.

[a,,b,c]Main effect means within a row without a common superscript letter differ ($P < 0.05$); presence of interaction means denotes a significant interaction ($P < 0.05$); [a,b,c,d,e,f]interaction means without a common superscript letter differ ($P < 0.05$).

Table 13. Effects of region and time of blood sampling on plasma osmolarity and oxygen (O_2) saturation of hair sheep offered water at 50% of ad libitum intake for wk (period 3)

		Region[1]				
	Time, h	MW	NW	SE	TX	SEM
Osmolality, mosm/L	0800	306.5[abc]	307.3[ab]	305.7[bc]	304.7[c]	0.83
	1400	308.4[a]	307.7[ab]	308.5[a]	308.3[a]	
O_2 saturation, %	0800	69.0[bc]	68.7[c]	69.3[bc]	70.3[bc]	1.35
	1400	69.7[bc]	71.4[ab]	74.3[a]	70.2[bc]	

[1]MW = Midwest; NW = Northwest; SE = Southeast; TX = Central Texas.

[a,b,c]Means for a significant region × time interaction (*P* < 0.05) without a common superscript letter differ (*P* < 0.05).

Table 14. *P* values for effects of breed (B), region (R), week (W), animal set, and initial age on serum metabolites of hair sheep offered water at 50% of ad libitum intake for 5 wk (period 3)

	Variable							
Source of variation[1]	Albumin, g/dL	Cholesterol, mg/dL	Creatinine, mg/dL	Glucose, mg/dL	Lactate, mg/dL	Total protein, g/dL	Triglycerides, mg/dL	Urea, mg/dL
B	0.919	0.536	0.007	0.007	0.720	0.655	0.403	0.440
R	0.694	0.026	0.735	0.658	0.485	0.623	0.524	0.459
W	0.046	0.004	<0.001	0.005	0.196	0.065	0.981	0.001
B*R	0.490	0.674	0.043	0.498	0.130	0.320	0.634	0.538
B*W	0.119	0.244	0.459	0.279	0.461	0.612	0.915	0.508
R*W	0.710	0.576	0.768	0.807	0.055	0.877	0.820	0.364
B*R*W	0.888	0.656	0.142	0.086	0.061	0.836	0.650	0.746
Set	<0.001	0.058	<0.001	0.006	<0.001	<0.001	0.725	0.008
Age	0.001	0.306	0.053	0.496	0.180	0.727	0.080	0.028
Covariate	<0.001	<0.001	<0.001	0.002	0.131	<0.001	<0.001	<0.001

[1]In each of 4 separate trials (9 wk each), a different set of sheep of 3 breeds (Dorper, Katahdin, and St. Croix) with each representing 4 U.S. climatic regions (the Midwest, Northwest, Southeast, and Central Texas) was used.

Table 15. Effects of breed, region, and week on serum metabolites of hair sheep offered water at 50% of ad libitum intake for 5 wk (period 3)

		Breed[1]				Region[2]					Week			
Variable	Breed	DOR	KAT	STC	SEM	MW	NW	SE	TX	SEM	2	4	5	SEM
Albumin, g/dL		2.70	2.69	2.68	0.030	2.70	2.69	2.72	2.66	0.035	2.68^{ab}	2.74^{a}	2.65^{b}	0.027
Cholesterol, mg/dL		71.9	71.9	69.3	1.84	75.8^{a}	66.6^{b}	71.8^{ab}	69.9^{ab}	2.13	70.1^{b}	73.9^{a}	69.1^{b}	1.35
Creatinine, mg/dL		0.962^{a}	0.924^{a}	0.868^{b}	0.018						0.973^{a}	0.916^{b}	0.865^{c}	0.013
	DOR					0.902^{bc}	1.050^{a}	0.936^{bc}	0.958^{ab}	0.033				
	KAT					0.964^{ab}	0.903^{bc}	0.938^{bc}	0.892^{bc}					
	STC					0.873^{bc}	0.854^{c}	0.849^{c}	0.896^{bc}					
Glucose, mg/dL		54.7^{b}	56.5^{b}	60.1^{a}	1.20	57.3	57.5	57.9	55.6	1.39	59.8^{a}	55.3^{b}	56.2^{b}	1.07
Lactate, mg/dL		23.5	22.9	22.2	1.13	21.8	24.6	22.3	22.9	1.29	22.4	24.2	22.2	0.95
Total protein, g/dL		7.36	7.24	7.27	0.096	7.35	7.31	7.33	7.16	0.110	7.27	7.43	7.17	0.084
Triglycerides, mg/dL		35.8	35.5	33.5	1.25	35.7	36.3	34.3	33.5	1.42	35.0	35.0	34.8	1.03
Urea, mg/dL		46.9	45.8	47.7	1.03	45.8	46.2	47.1	48.4	1.16	47.9^{a}	48.2^{a}	44.5^{b}	0.81

[1]DOR = Dorper; KAT = Katahdin; STC = St. Croix.

[2]MW = Midwest; NW = Northwest; SE = Southeast; TX = Central Texas.

^{a,b,c}Main effect means within a row without a common superscript letter differ ($P < 0.05$); presence of interaction means denotes a significant interaction ($P < 0.05$); ^{a,b,c}interaction means without a common superscript letter differ ($P < 0.05$).

Table 16. *P* values for effects of breed (B), region (R), time of blood sampling (T), animal set, and initial age on blood characteristics of hair sheep offered water at 50% of ad libitum intake during the last 2 wk of period 3

	Variable[1]				
Source of variation[2]	Osmolality, mosm/L	PCV, %	Hb concentration, g/dL	O_2 saturation, %	O_2 concentration, mmol/L
B	0.071	0.001	0.011	0.066	0.001
R	0.496	0.010	0.024	0.458	0.147
T	0.780	0.143	0.015	0.035	0.531
B*R	0.138	0.115	0.062	0.571	0.787
B*T	0.083	0.288	0.242	0.409	0.228
R*T	0.014	0.430	0.263	0.496	0.812
B*R*T	0.554	0.539	0.153	0.059	0.020
Set	<0.001	0.052	0.002	0.001	<0.001
Age	0.621	0.800	0.818	0.314	0.482
Covariate	0.142	<0.001	<0.001	<0.001	<0.001

[1] PCV = packed cell volume; Hb = hemoglobin; O_2 = oxygen.

[2]In each of 4 separate trials (9 wk each), a different set of sheep of 3 breeds (Dorper, Katahdin, and St. Croix) with each representing 4 U.S. climatic regions (the Midwest, Northwest, Southeast, and Central Texas) was used and blood samples were collected twice weekly (Wednesday at 0800 h and Thursday at 1400 h).

Table 17. Effects of breed, region, and time of blood sampling on blood characteristics of hair sheep offered water at 50% of ad libitum intake during the last 2 wk of period 3

		Breed[1]				Region[2]					Time, h		
Variable[3]	Time, h	DOR	KAT	STC	SEM	MW	NW	SE	TX	SEM	0800	1400	SEM
Osmolality, mosm/L		305.5	307.8	305.3	0.84								
	0800					305.8[ab]	308.2[a]	305.2[b]	305.2[ab]	1.07			
	1400					305.6[ab]	306.3[ab]	305.5[ab]	307.6[ab]				
PCV, %		31.6[b]	31.8[b]	33.6[a]	0.40	32.3[ab]	31.1[b]	32.9[a]	33.1[a]	0.45	32.5	32.2	0.25
Hb concentration, g/dL		12.02[b]	12.01[b]	12.60[a]	0.151	12.26[a]	11.75[b]	12.39[a]	12.44[a]	0.175	12.28[a]	12.14[b]	0.090
O_2 saturation, %		69.8	69.4	73.2	1.22	70.2	70.5	72.7	69.8	1.42	69.7[b]	71.9[a]	0.86

[1]DOR = Dorper; KAT = Katahdin; STC = St. Croix.
[2]MW = Midwest; NW = Northwest; SE = Southeast; TX = Central Texas.
[3]PCV = packed cell volume; Hb = hemoglobin; O_2 = oxygen.
[a,b]Main effect means within a row without a common superscript letter differ ($P < 0.05$); presence of interaction means denotes a significant interaction ($P < 0.05$); [a,b]interaction means without a common superscript letter differ ($P < 0.05$).

Table 18. *P* values for effects of breed (B), region (R), animal set, and initial age on serum metabolites of hair sheep offered water at 50% of ad libitum intake during the last 2 wk of period 3

	Variable							
Source of variation[1]	Albumin, g/dL	Cholesterol, mg/dL	Creatinine, mg/dL	Glucose, mg/dL	Lactate, mg/dL	Total protein, g/dL	Triglycerides, mg/dL	Urea, mg/dL
B	0.459	0.850	0.007	0.014	0.807	0.570	0.263	0.145
R	0.551	0.038	0.732	0.450	0.518	0.781	0.435	0.212
B*R	0.804	0.962	0.015	0.589	0.056	0.660	0.706	0.648
Set	0.014	0.011	0.007	0.117	<0.001	0.018	0.356	0.436
Age	0.007	0.232	0.041	0.852	0.257	0.901	0.085	0.026
Covariate	0.001	<0.001	<0.001	0.006	0.202	0.035	<0.001	<0.001

[1]In each of 4 separate trials (9 wk each), a different set of sheep of 3 breeds (Dorper, Katahdin, and St. Croix) with each representing 4 U.S. climatic regions (the Midwest, Northwest, Southeast, and Central Texas) was used.

Table 19. Effects of breed and region on serum metabolites of hair sheep offered water at 50% of ad libitum intake during the last 2 wk of period 3

		Breed[1]				Region[2]				
Variable	Breed	DOR	KAT	STC	SEM	MW	NW	SE	TX	SEM
Albumin, g/dL		2.71	2.65	2.71	0.041	2.70	2.68	2.74	2.65	0.047
Cholesterol, mg/dL		72.3	71.5	70.6	2.09	76.3[a]	66.7[b]	73.1[ab]	69.7[ab]	2.47
Creatinine, mg/dL		0.938[a]	0.896[a]	0.838[b]	0.020					
	DOR					0.853[bcd]	1.034[a]	0.924[bc]	0.942[abc]	0.037
	KAT					0.949[ab]	0.874[bcd]	0.903[bcd]	0.857[bcd]	
	STC					0.846[cd]	0.820[d]	0.816[d]	0.870[bcd]	
Glucose, mg/dL		53.9[b]	54.0[b]	59.2[a]	1.42	56.6	55.8	56.9	53.5	1.64
Lactate, mg/dL		23.5	23.6	22.5	1.35	21.7	24.7	23.0	23.4	1.53
Total protein, g/dL		7.32	7.19	7.37	0.119	7.29	7.36	7.35	7.18	0.137
Triglycerides, mg/dL		36.0	35.7	32.7	1.41	35.6	36.7	34.0	33.0	1.61
Urea, mg/dL		46.0	44.9	48.2	1.18	44.7	45.6	46.4	48.8	1.35

[1]DOR = Dorper; KAT = Katahdin; STC = St. Croix.

[2]MW = Midwest; NW = Northwest; SE = Southeast; TX = Central Texas.

[a,b]Main effect means within a row without a common superscript letter differ ($P < 0.05$); presence of interaction means denotes a significant interaction ($P < 0.05$); [a,b,c,d]interaction means without a common superscript letter differ ($P < 0.05$).

Table 20. Spearman rank correlation coefficients (*sr*) between periods and between weeks in period 3 for plasma osmolality in mosm/L at 2 times of blood sampling of hair sheep[1]

			Breed[2]							
			DOR		KAT		STC		Overall	
Variable		Time, h	*sr*	*P*	*sr*	*P*	*sr*	*P*	*sr*	*P*
Periods	1 and 2	0800	0.48	<0.001	0.29	0.006	0.35	0.001	0.38	<0.001
		1400	0.34	0.002	0.12	0.263	0.14	0.193	0.20	0.002
		Average	0.50	<0.001	0.18	0.103	0.35	0.001	0.34	<0.001
	1 and 3	0800	0.38	0.001	0.03	0.762	0.12	0.258	0.17	0.006
		1400	0.30	0.005	0.04	0.718	0.20	0.064	0.19	0.003
		Average	0.45	<0.001	0.07	0.497	0.28	0.008	0.26	<0.001
	2 and 3	0800	0.28	0.008	0.12	0.281	0.39	<0.001	0.28	<0.001
		1400	0.33	0.002	0.24	0.029	0.29	0.007	0.29	<0.001
		Average	0.47	<0.001	0.27	0.011	0.50	<0.001	0.42	<0.001
Weeks	1 and 2	0800	0.24	0.190	0.16	0.387	0.36	0.045	0.22	0.028
		1400	0.41	0.006	0.35	0.021	0.38	0.011	0.38	<0.001
		Average	0.46	0.002	0.37	0.015	0.50	0.001	0.44	<0.001
	1 and 3	0800	0.05	0.767	0.13	0.472	0.32	0.078	0.06	0.592
		1400	0.61	<0.001	0.06	0.683	0.61	<0.001	0.43	<0.001
		Average	0.43	0.004	0.11	0.481	0.56	<0.001	0.38	<0.001
	1 and 4	0800	0.06	0.758	0.03	0.857	0.33	0.061	0.15	0.144
		1400	0.44	0.003	0.14	0.380	0.11	0.475	0.24	0.006
		Average	0.41	0.007	0.19	0.229	0.39	0.009	0.31	<0.001
	1 and 5	0800	0.24	0.181	0.25	0.164	0.54	0.002	0.33	0.001
		1400	0.49	0.001	0.30	0.054	0.37	0.015	0.41	<0.001
		Average	0.46	0.002	0.28	0.074	0.35	0.020	0.35	<0.001
	2 and 3	0800	0.32	0.037	0.36	0.019	0.34	0.024	0.33	<0.001
		1400	0.35	0.022	0.69	<0.001	0.33	0.028	0.45	<0.001

	Average	0.47	0.002	0.57	<0.001	0.47	0.001	0.49	<0.001
2 and 4	0800	0.28	0.066	0.48	0.001	0.09	0.551	0.30	0.001
	1400	0.35	0.021	0.45	0.003	0.04	0.804	0.29	0.001
	Average	0.34	0.027	0.51	0.0001	0.12	0.442	0.31	<0.001
2 and 5	0800	0.10	0.527	0.16	0.302	0.15	0.324	0.15	0.096
	1400	0.39	0.009	0.44	0.004	0.32	0.035	0.38	<0.001
	Average	0.33	0.029	0.27	0.083	0.37	0.015	0.32	<0.001
3 and 4	0800	0.39	0.010	0.45	0.003	0.47	0.001	0.43	<0.001
	1400	0.47	0.002	0.52	<0.001	0.11	0.463	0.39	<0.001
	Average	0.51	0.001	0.62	<0.001	0.39	0.009	0.51	<0.001
3 and 5	0800	0.16	0.296	0.16	0.326	0.03	0.849	0.11	0.195
	1400	0.40	0.008	0.28	0.075	0.31	0.041	0.35	<0.001
	Average	0.36	0.018	0.25	0.119	0.22	0.148	0.28	0.001
4 and 5	0800	0.22	0.151	0.51	0.001	0.19	0.218	0.32	<0.001
	1400	0.58	<0.001	0.64	<0.001	0.33	0.028	0.55	<0.001
	Average	0.54	<0.001	0.62	<0.001	0.45	0.003	0.54	<0.001

[1]The sheep were offered water ad libitum intake in period 1, 75% of ad libitum intake in period 2, and 50% of ad libitum intake in period 3.
[2]DOR = Dorper; KAT = Katahdin; STC = St. Croix.

Table 21. Spearman rank correlation coefficients (*sr*) between periods and between weeks in period 3 for blood packed cell volume in percentage at 2 times of blood sampling of hair sheep[1]

			Breed[2]							
			DOR		KAT		STC		Overall	
Variable		Time, h	*sr*	*P*	*sr*	*P*	*sr*	*P*	*sr*	*P*
Periods	1 and 2	0800	0.56	<0.001	0.64	<0.001	0.64	<0.001	0.62	<0.001
		1400	0.66	<0.001	0.57	<0.001	0.54	<0.001	0.58	<0.001
		Average	0.69	<0.001	0.70	<0.001	0.70	<0.001	0.70	<0.001
	1 and 3	0800	0.56	<0.001	0.48	<0.001	0.44	<0.001	0.49	<0.001
		1400	0.40	<0.001	0.53	<0.001	0.22	0.054	0.38	<0.001
		Average	0.49	<0.001	0.49	<0.001	0.43	<0.001	0.46	<0.001
	2 and 3	0800	0.68	<0.001	0.67	<0.001	0.50	<0.001	0.62	<0.001
		1400	0.51	<0.001	0.67	<0.001	0.46	<0.001	0.55	<0.001
		Average	0.68	<0.001	0.76	<0.001	0.59	<0.001	0.69	<0.001
Weeks	1 and 2	0800	0.76	<0.001	0.43	0.014	0.63	<0.001	0.62	<0.001
		1400	0.69	<0.001	0.72	<0.001	0.67	<0.001	0.68	<0.001
		Average	0.76	<0.001	0.73	<0.001	0.64	<0.001	0.72	<0.001
	1 and 3	0800	0.76	<0.001	0.52	0.003	0.29	0.108	0.54	<0.001
		1400	0.64	<0.001	0.70	<0.001	0.54	0.001	0.63	<0.001
		Average	0.65	<0.001	0.52	<0.001	0.49	0.001	0.65	<0.001
	1 and 4	0800	0.73	<0.001	0.75	<0.001	0.45	0.010	0.65	<0.001
		1400	0.59	<0.001	0.66	<0.001	0.46	0.002	0.56	<0.001
		Average	0.67	<0.001	0.70	<0.001	0.49	0.001	0.67	<0.001
	1 and 5	0800	0.66	<0.001	0.39	0.030	0.60	<0.001	0.52	<0.001
		1400	0.51	<0.001	0.43	0.005	0.45	0.003	0.45	<0.001
		Average	0.61	<0.001	0.44	0.003	0.64	<0.001	0.61	<0.001
	2 and 3	0800	0.73	<0.001	0.52	<0.001	0.59	<0.001	0.61	<0.001
		1400	0.86	<0.001	0.58	0.001	0.65	<0.001	0.71	<0.001

	Average	0.76	<0.001	0.51	<0.001	0.61	<0.001	0.76	<0.001
2 and 4	0800	0.57	<0.001	0.64	<0.001	0.55	<0.001	0.59	<0.001
	1400	0.74	<0.001	0.57	<0.001	0.38	0.010	0.58	<0.001
	Average	0.71	<0.001	0.73	<0.001	0.57	<0.001	0.71	<0.001
2 and 5	0800	0.56	<0.001	0.54	<0.001	0.54	<0.001	0.54	<0.001
	1400	0.56	<0.001	0.45	0.004	0.47	0.001	0.49	<0.001
	Average	0.68	<0.001	0.58	<0.001	0.60	<0.001	0.68	<0.001
3 and 4	0800	0.65	<0.001	0.54	<0.001	0.51	<0.001	0.56	<0.001
	1400	0.78	<0.001	0.58	0.001	0.56	<0.001	0.65	<0.001
	Average	0.72	<0.001	0.59	<0.001	0.62	<0.001	0.72	<0.001
3 and 5	0800	0.56	<0.001	0.46	0.002	0.51	<0.001	0.49	<0.001
	1400	0.53	0.003	0.53	0.003	0.50	0.002	0.60	<0.001
	Average	0.65	<0.001	0.52	<0.001	0.55	<0.001	0.65	<0.001
4 and 5	0800	0.67	<0.001	0.70	<0.001	0.52	<0.001	0.65	<0.001
	1400	0.65	<0.001	0.65	<0.001	0.60	<0.001	0.64	<0.001
	Average	0.74	<0.001	0.78	<0.001	0.67	<0.001	0.74	<0.001

[1]The sheep were offered water ad libitum intake in period 1, 75% of ad libitum intake in period 2, and 50% of ad libitum intake in period 3.
[2]DOR = Dorper; KAT = Katahdin; STC = St. Croix.

Table 22. Spearman rank correlation coefficients (*sr*) between periods and between weeks in period 3 for blood hemoglobin concentration in g/dL at 2 times of blood sampling of hair sheep[1]

			Breed[2]							
			DOR		KAT		STC		Overall	
Variable		Time, h	*sr*	*P*	*sr*	*P*	*sr*	*P*	*sr*	*P*
Periods	1 and 2	0800	0.68	<0.001	0.70	<0.001	0.71	<0.001	0.69	<0.001
		1400	0.70	<0.001	0.62	<0.001	0.67	<0.001	0.66	<0.001
		Average	0.72	<0.001	0.75	<0.001	0.78	<0.001	0.75	<0.001
	1 and 3	0800	0.67	<0.001	0.50	<0.001	0.55	<0.001	0.54	<0.001
		1400	0.61	<0.001	0.63	<0.001	0.39	0.001	0.56	<0.001
		Average	0.70	<0.001	0.57	<0.001	0.54	<0.001	0.59	<0.001
	2 and 3	0800	0.72	<0.001	0.76	<0.001	0.58	<0.001	0.68	<0.001
		1400	0.63	<0.001	0.76	<0.001	0.62	<0.001	0.66	<0.001
		Average	0.70	<0.001	0.86	<0.001	0.63	<0.001	0.74	<0.001
Weeks	1 and 2	0800	0.79	<0.001	0.53	0.002	0.71	<0.001	0.69	<0.001
		1400	0.77	<0.001	0.82	<0.001	0.70	<0.001	0.76	<0.001
		Average	0.81	<0.001	0.78	<0.001	0.73	<0.001	0.78	<0.001
	1 and 3	0800	0.79	<0.001	0.53	0.002	0.48	0.006	0.60	<0.001
		1400	0.75	<0.001	0.66	<0.001	0.77	<0.001	0.74	<0.001
		Average	0.76	<0.001	0.70	<0.001	0.68	<0.001	0.72	<0.001
	1 and 4	0800	0.81	<0.001	0.71	<0.001	0.60	<0.001	0.72	<0.001
		1400	0.67	<0.001	0.76	<0.001	0.65	<0.001	0.68	<0.001
		Average	0.74	<0.001	0.73	<0.001	0.71	<0.001	0.73	<0.001
	1 and 5	0800	0.80	<0.001	0.33	0.002	0.58	<0.001	0.55	<0.001
		1400	0.60	<0.001	0.62	<0.001	0.68	<0.001	0.61	<0.001
		Average	0.72	<0.001	0.53	<0.001	0.67	<0.001	0.62	<0.001
	2 and 3	0800	0.78	<0.001	0.55	<0.001	0.81	<0.001	0.69	<0.001
		1400	0.90	<0.001	0.67	<0.001	0.70	<0.001	0.75	<0.001

	Average	0.89	<0.001	0.72	<0.001	0.76	<0.001	0.81	<0.001
2 and 4	0800	0.70	<0.001	0.76	<0.001	0.74	<0.001	0.73	<0.001
	1400	0.79	<0.001	0.68	<0.001	0.55	<0.001	0.66	<0.001
	Average	0.81	<0.001	0.80	<0.001	0.71	<0.001	0.77	<0.001
2 and 5	0800	0.67	<0.001	0.69	<0.001	0.64	<0.001	0.64	<0.001
	1400	0.71	<0.001	0.55	<0.001	0.53	<0.001	0.59	<0.001
	Average	0.75	<0.001	0.68	<0.001	0.60	<0.001	0.66	<0.001
3 and 4	0800	0.75	<0.001	0.53	<0.001	0.69	<0.001	0.64	<0.001
	1400	0.86	<0.001	0.72	<0.001	0.68	<0.001	0.76	<0.001
	Average	0.88	<0.001	0.72	<0.001	0.76	<0.001	0.80	<0.001
3 and 5	0800	0.71	<0.001	0.43	0.004	0.61	<0.001	0.56	<0.001
	1400	0.72	<0.001	0.61	<0.001	0.58	<0.001	0.64	<0.001
	Average	0.81	<0.001	0.52	<0.001	0.62	<0.001	0.65	<0.001
4 and 5	0800	0.72	<0.001	0.76	<0.001	0.63	<0.001	0.71	<0.001
	1400	0.73	<0.001	0.59	<0.001	0.68	<0.001	0.66	<0.001
	Average	0.80	<0.001	0.76	<0.001	0.75	<0.001	0.76	<0.001

[1]The sheep were offered water ad libitum intake in period 1, 75% of ad libitum intake in period 2, and 50% of ad libitum intake in period 3.
[2]DOR = Dorper; KAT = Katahdin; STC = St. Croix.

Table 23. Homogeneity of variance in plasma osmolality and blood packed cell volume (PCV), hemoglobin (Hb) concentration, oxygen (O_2) saturation, and O_2 concentration at 2 times of blood sampling in the last 2 wk of offering water at 50% of ad libitum intake to hair sheep[1]

			SD[2]		
Variable	Time	*P*[3]	DOR	KAT	STC
Osmolality, mosm/L	0800	0.005	6.91	8.87	5.34
	1400	0.062	7.38	8.97	6.25
PCV, %	0800	0.019	3.43	3.93	2.54
	1400	0.056	3.62	3.27	2.50
Hb concentration, g/dL	0800	0.026	1.46	1.36	0.97
	1400	0.077	1.37	1.24	0.97
O_2 saturation, %	0800	0.148			
	1400	0.474			
O_2 concentration, mmol/L	0800	0.692			
	1400	0.898			

[1]DOR = Dorper; KAT = Katahdin; STC = St. Croix.
[2]SD = standard deviation (shown for $P < 0.05$).
[3]*P* value for the Bartlett test.

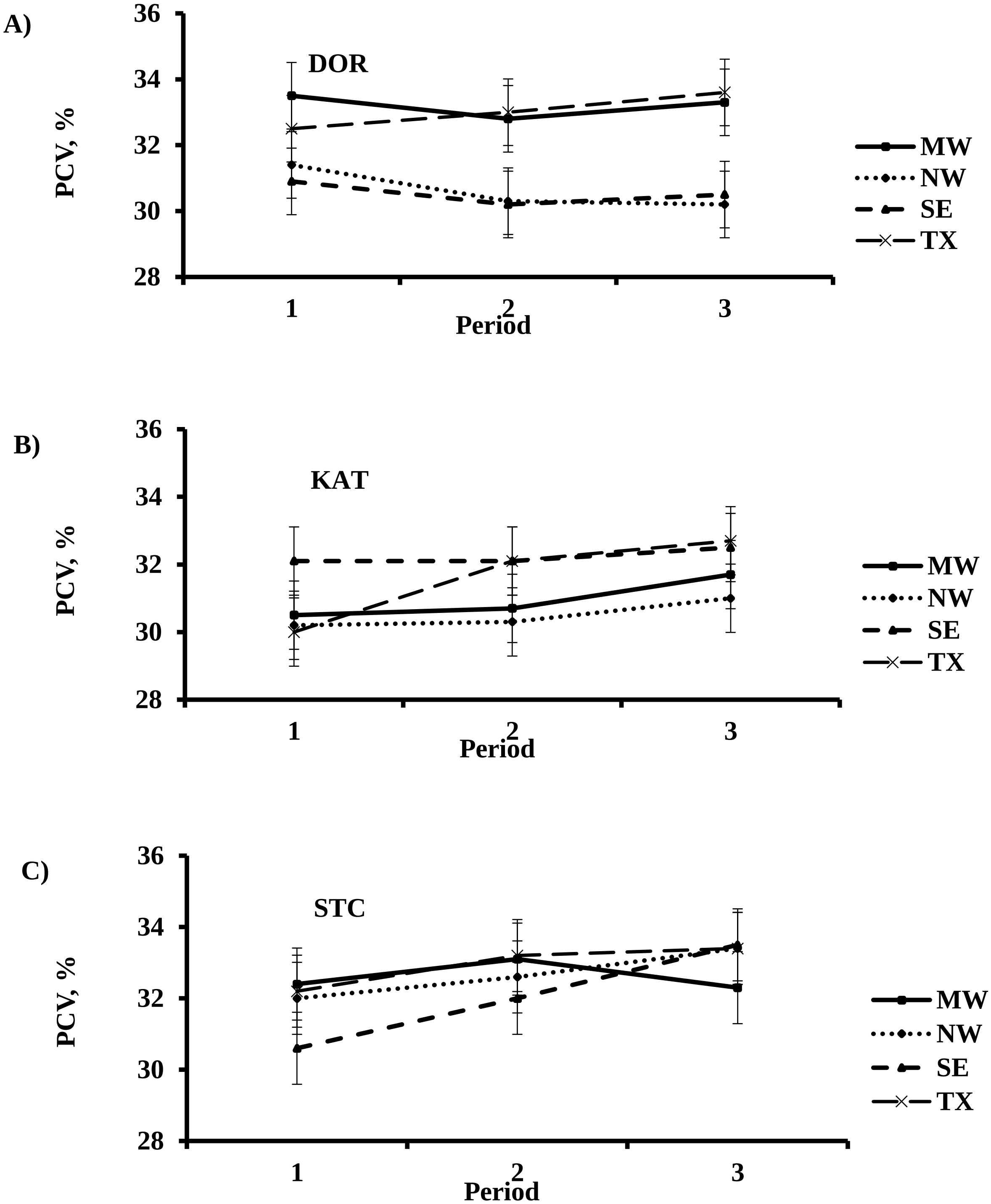


Figure 1. Packed cell volume (PCV) of Dorper (DOR), Katahdin (KAT), and St. Croix (STC) sheep from the Midwest (MW), Northwest (NW), Southeast (SE), and Central Texas (TX) when offered water ad libitum (period 1), at 75% of ad libitum intake (period 2), and at 50% of ad libitum intake (period 3).

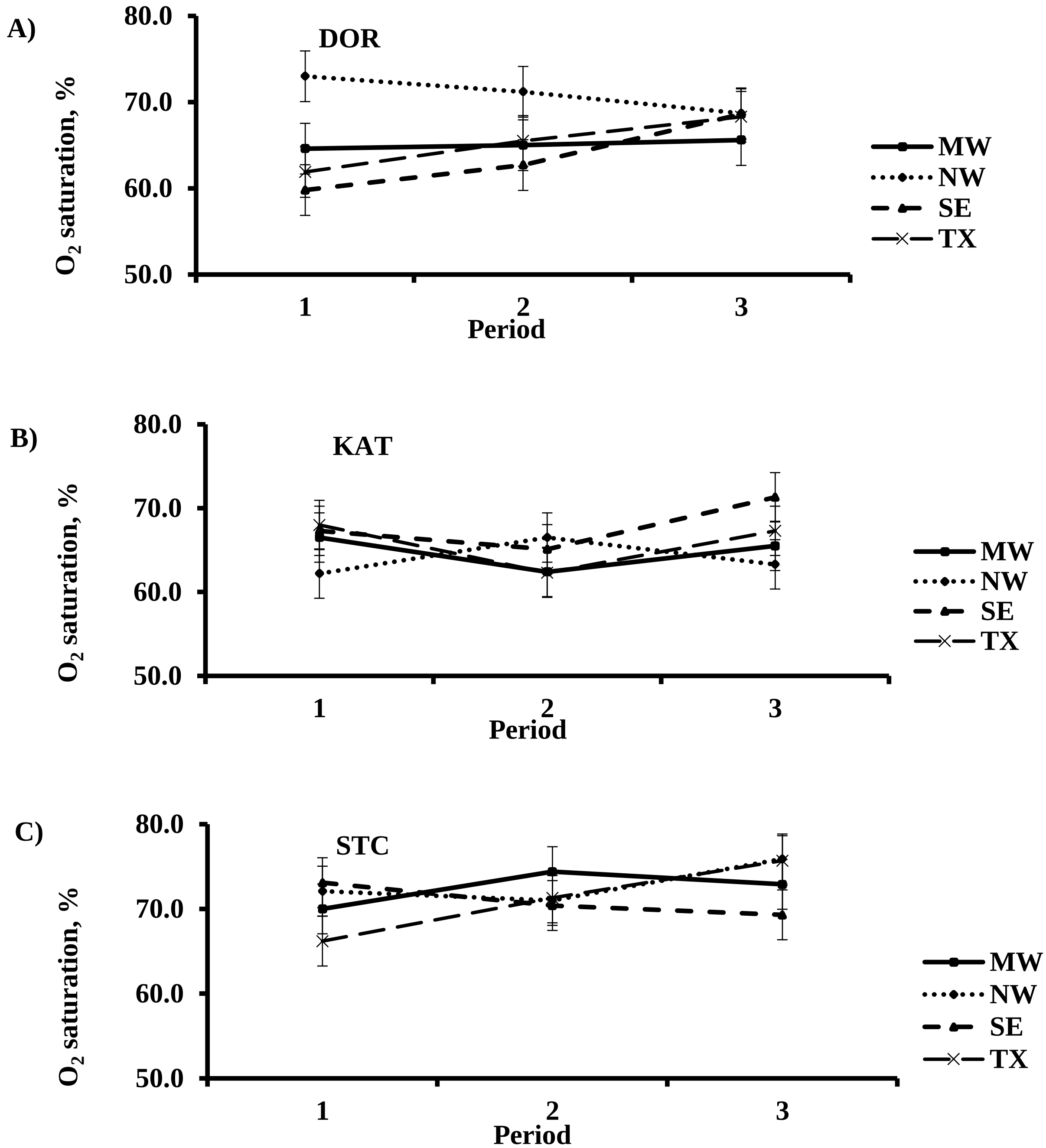
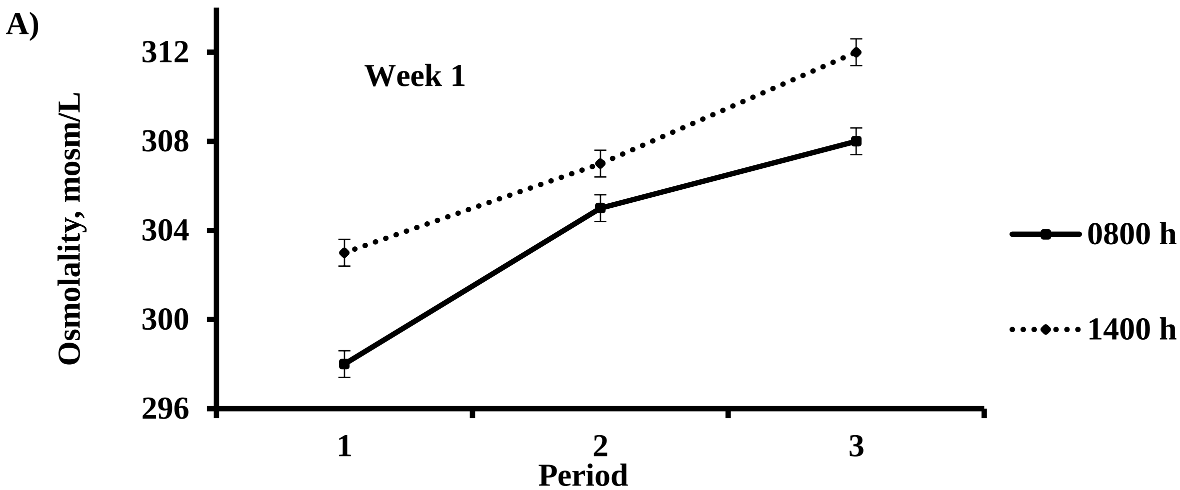


Figure 2. Oxygen saturation of hemoglobin of Dorper (DOR), Katahdin (KAT), and St. Croix (STC) sheep from the Midwest (MW), Northwest (NW), Southeast (SE), and Central Texas (TX) when offered water ad libitum (period 1), at 75% of ad libitum intake (period 2), and at 50% of ad libitum intake (period 3).



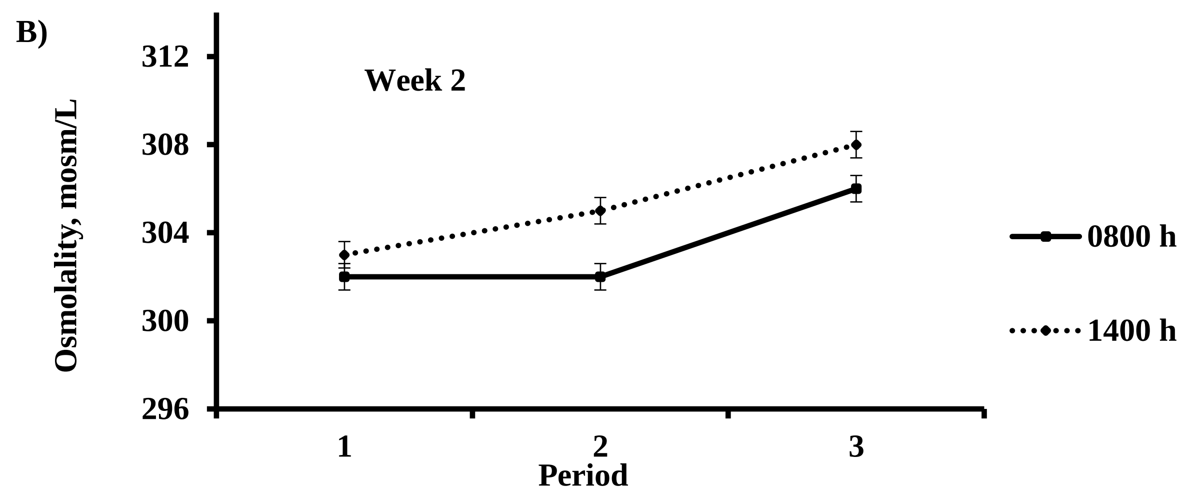


Figure 3. Differences between time of blood sampling among weeks within period in plasma osmolality of hair sheep offered water ad libitum (period 1), at 75% of ad libitum intake (period 2), and at 50% of ad libitum intake (period 3).

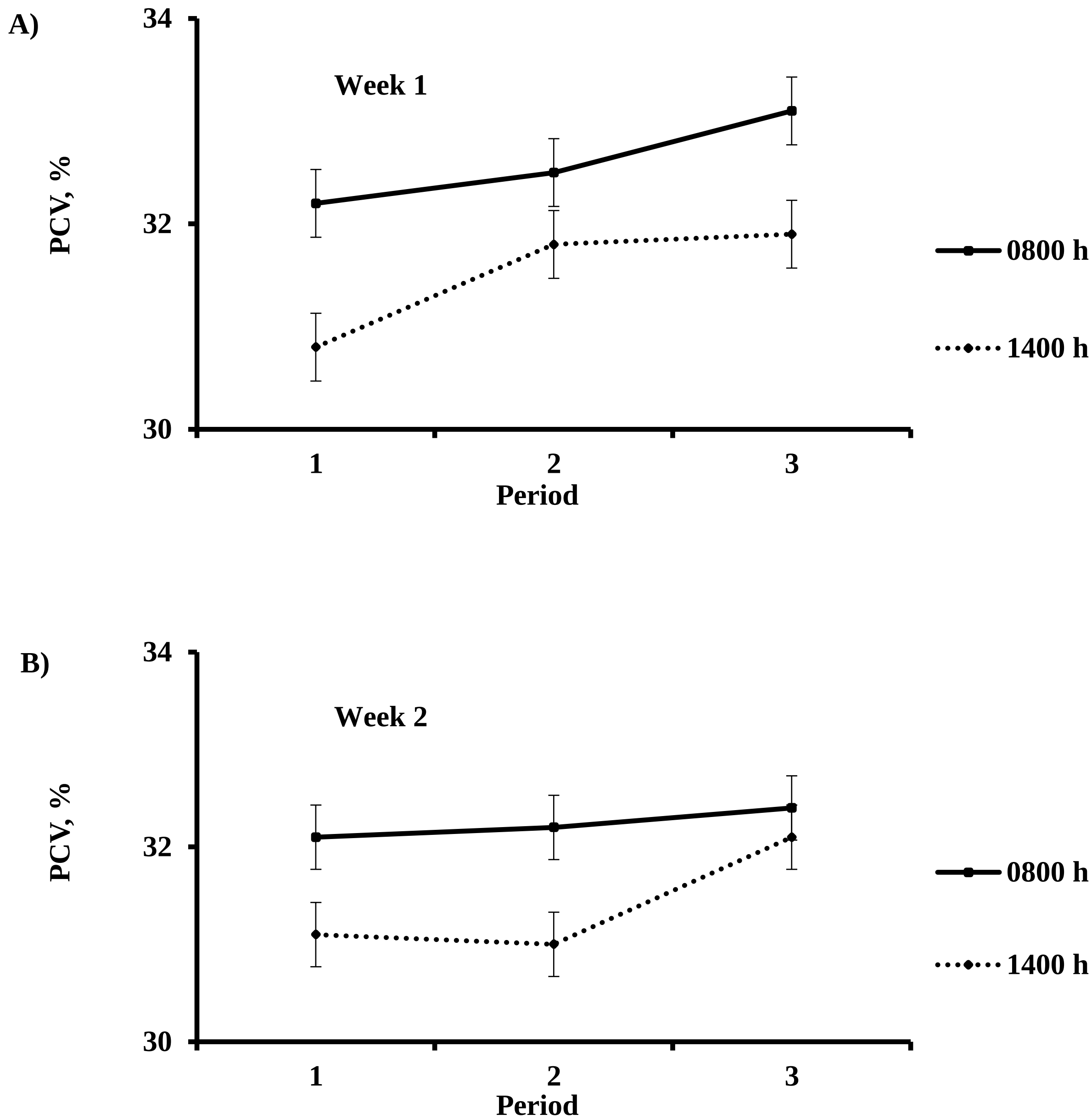


Figure 4. Differences between time of blood sampling among weeks within period in packed cell volume (PCV) of hair sheep offered water ad libitum (period 1), at 75% of ad libitum intake (period 2), and at 50% of ad libitum intake (period 3).

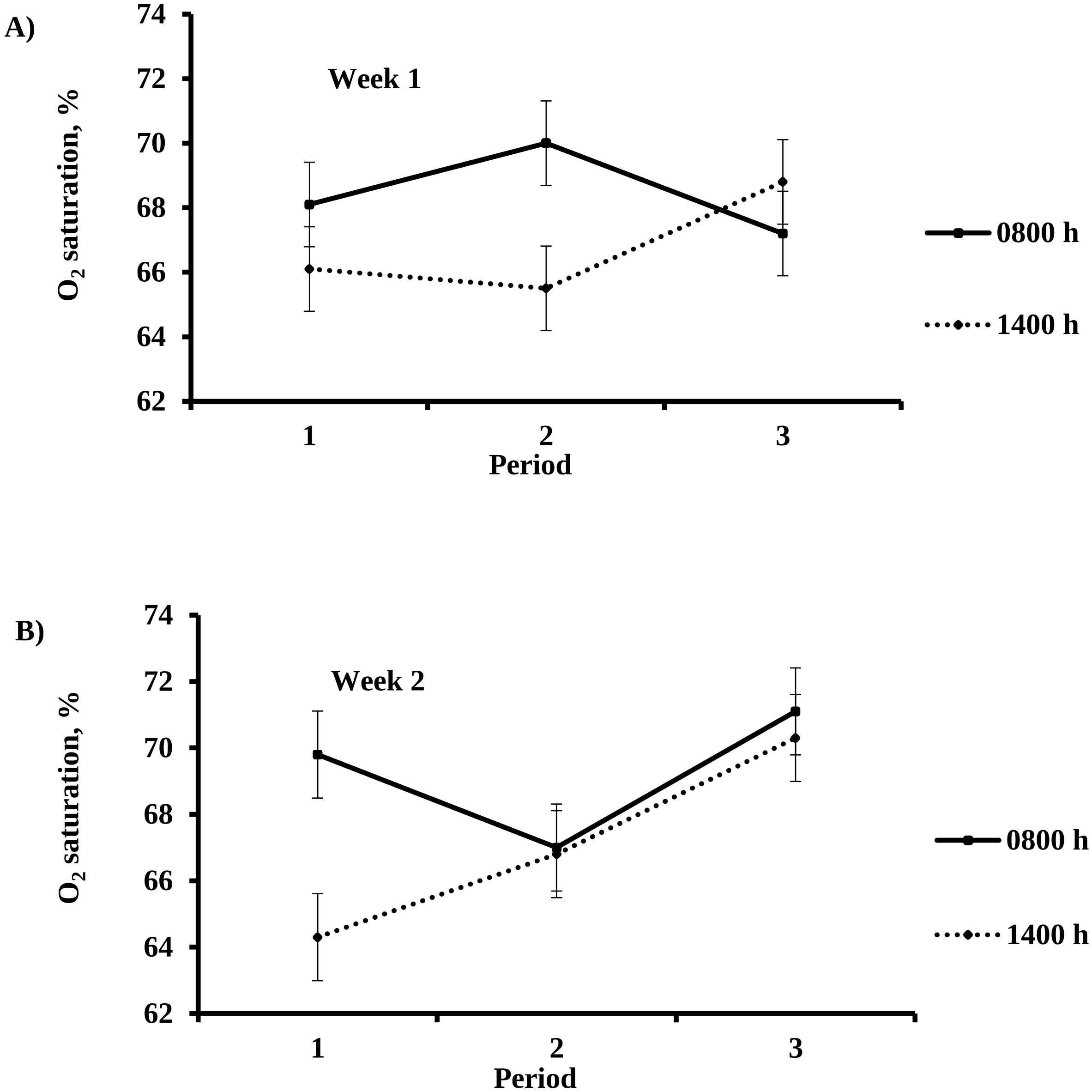


Figure 5. Differences between time of blood sampling among weeks within period in oxygen saturation of hemoglobin of hair sheep offered water ad libitum (period 1), at 75% of ad libitum intake (period 2), and at 50% of ad libitum intake (period 3).

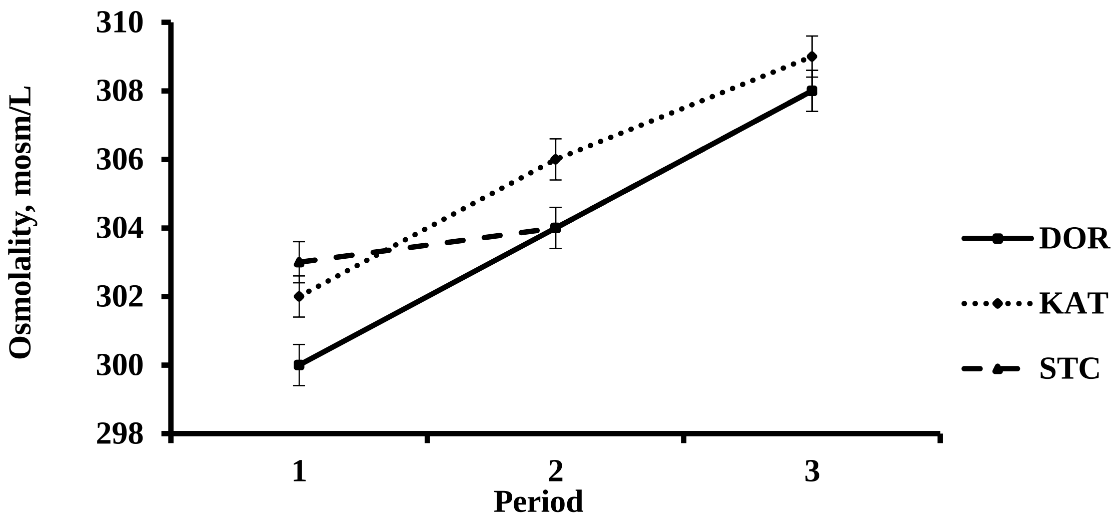


Figure 6. Plasma osmolality of Dorper (DOR), Katahdin (KAT), and St. Croix (STC) sheep offered water ad libitum (period 1), at 75% of ad libitum intake (period 2), and at 50% of ad libitum intake (period 3).

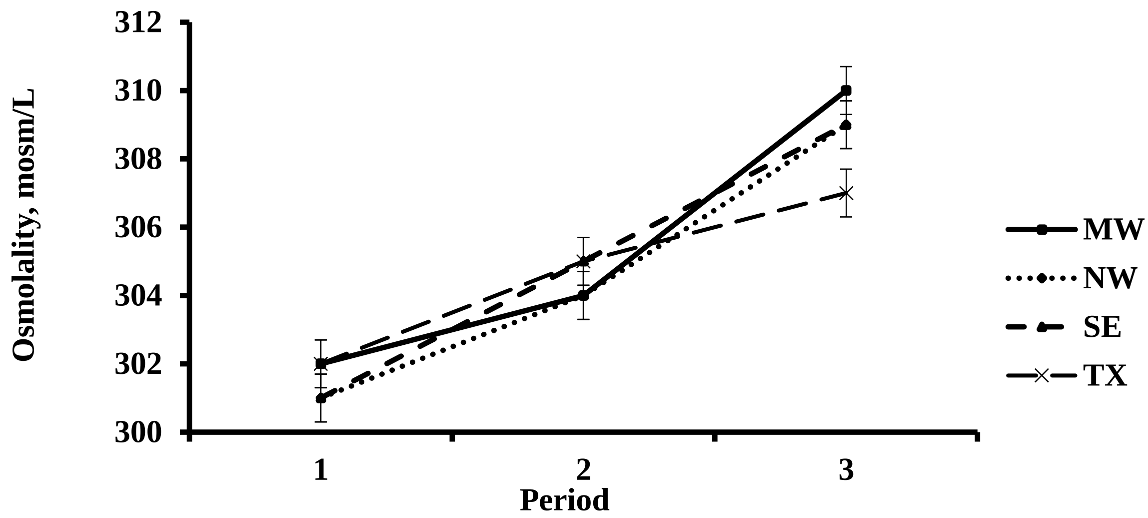


Figure 7. Plasma osmolality of hair sheep from the Midwest (MW), Northwest (NW), Southeast (SE), and Central Texas (TX) when offered water ad libitum (period 1), at 75% of ad libitum intake (period 2), and at 50% of ad libitum intake (period 3).

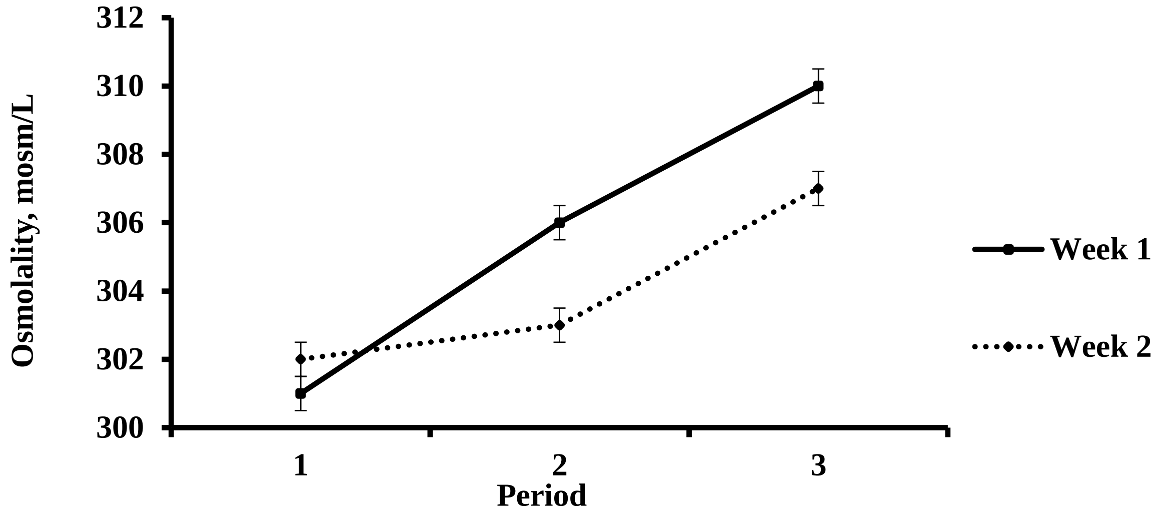


Figure 8. Differences between weeks within period in plasma osmolality of hair sheep offered water ad libitum (period 1), at 75% of ad libitum intake (period 2), and at 50% of ad libitum intake (period 3).

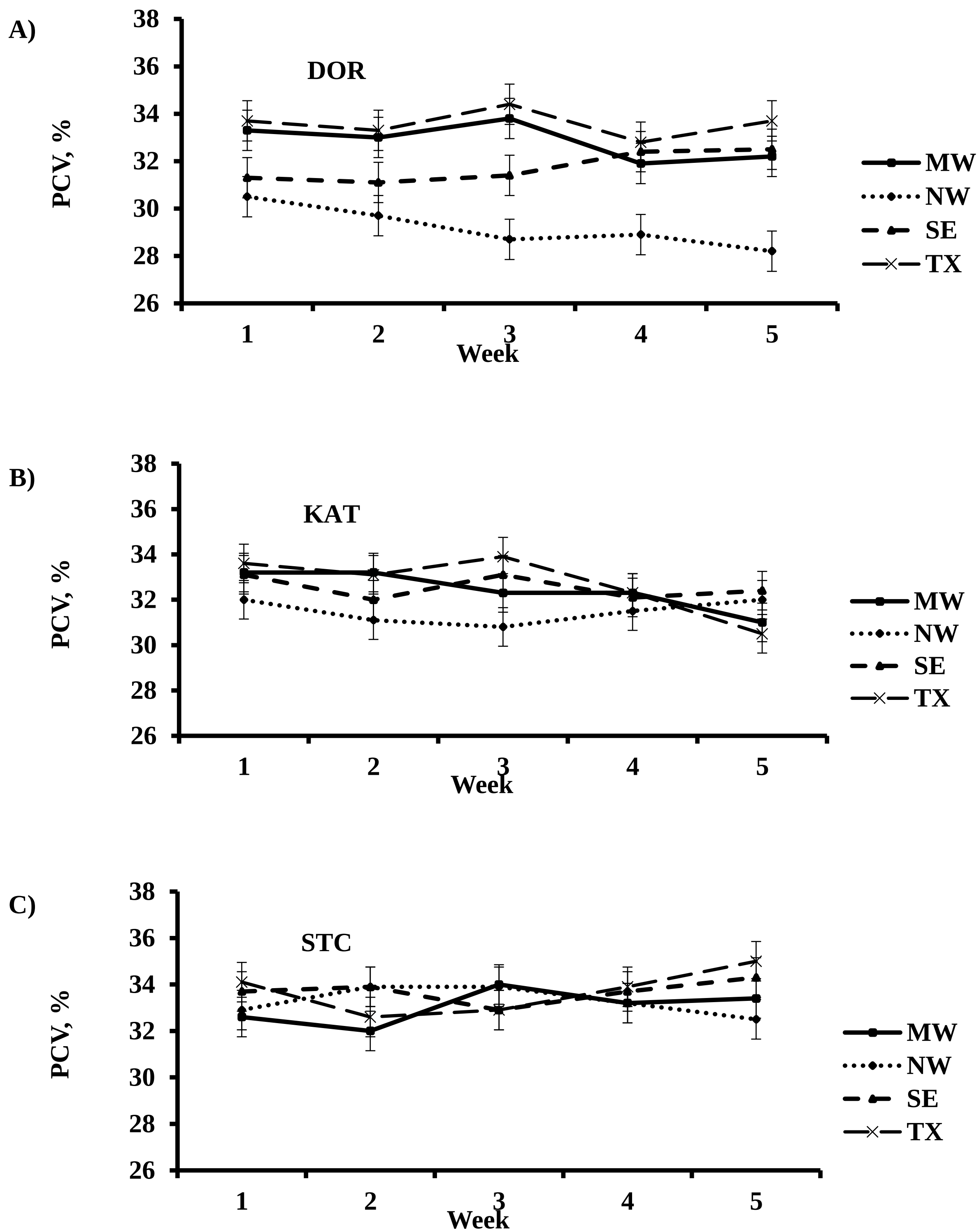


Figure 9. Weekly packed cell volume (PCV) of Dorper (DOR), Katahdin (KAT), and St. Croix (STC) sheep from the Midwest (MW), Northwest (NW), Southeast (SE), and Central Texas (TX) when offered water at 50% of ad libitum intake in period 3.

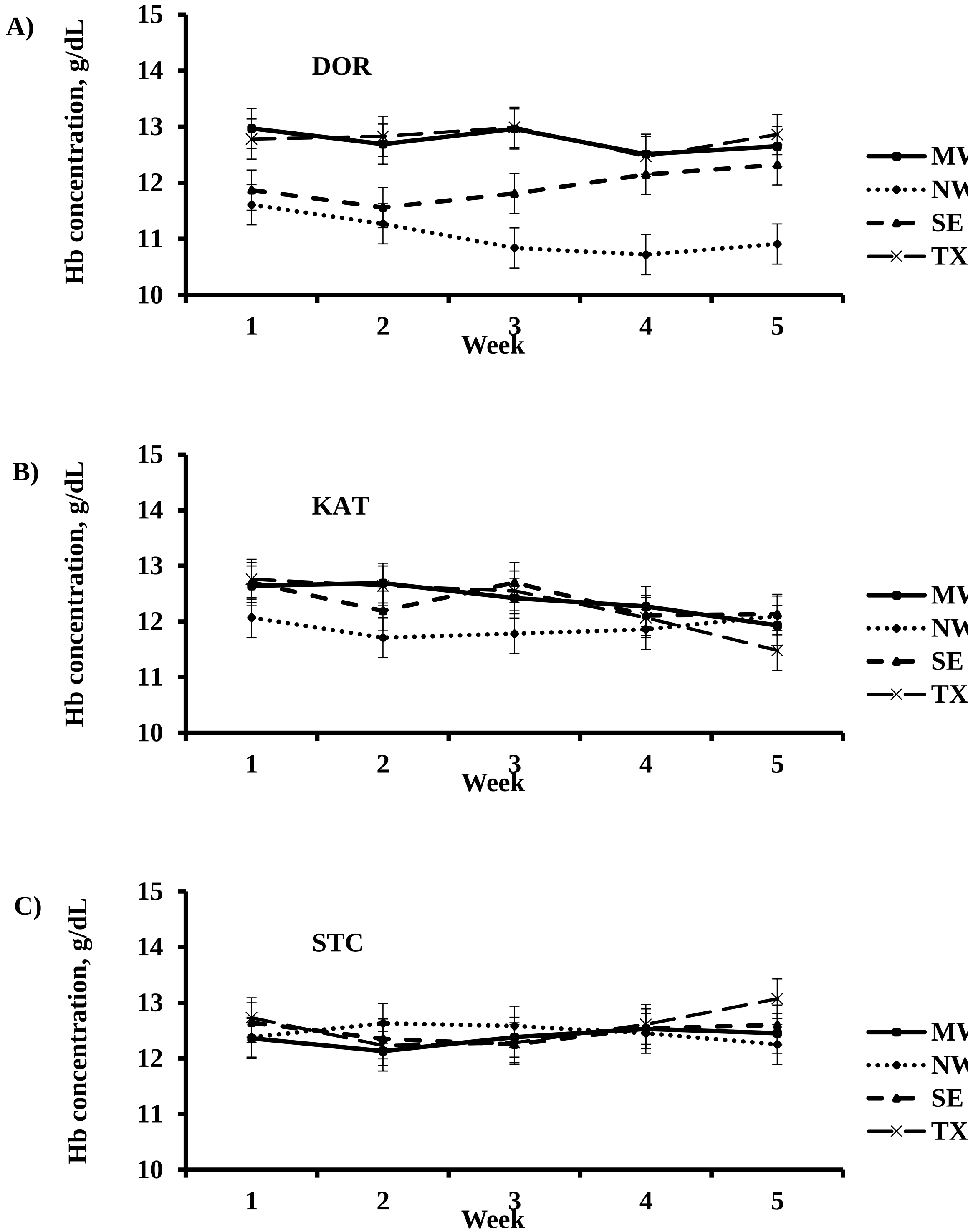


Figure 10. Weekly hemoglobin (Hb) concentration of Dorper (DOR), Katahdin (KAT), and St. Croix (STC) sheep from the Midwest (MW), Northwest (NW), Southeast (SE), and Central Texas (TX) when offered water at 50% of ad libitum intake in period 3.

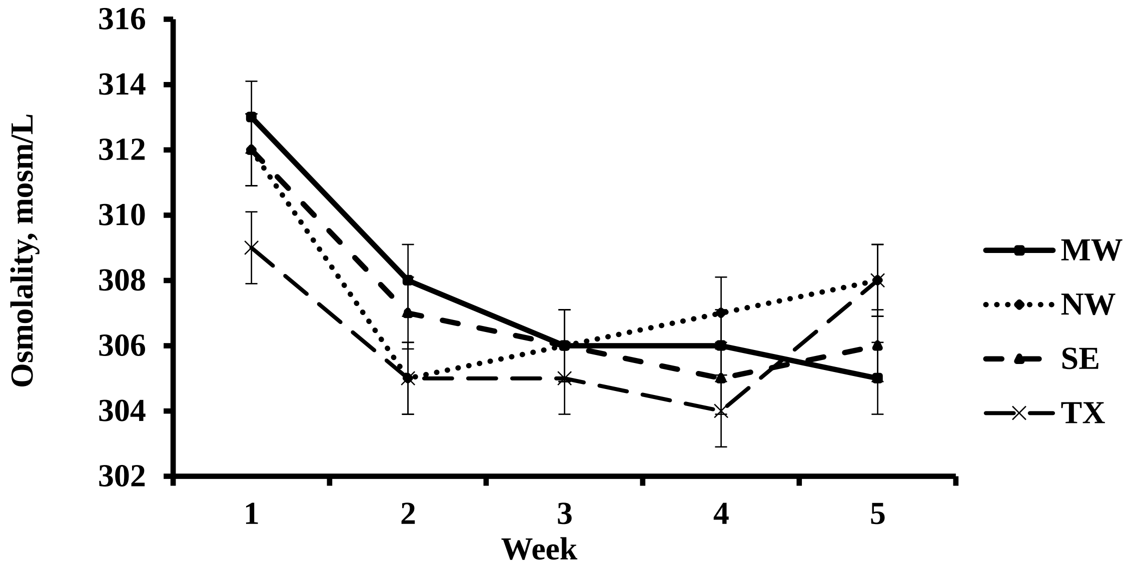


Figure 11. Weekly plasma osomlality of hair sheep from the Midwest (MW), Northwest (NW), Southeast (SE), and Central Texas (TX) when offered water at 50% of ad libitum intake in period 3.

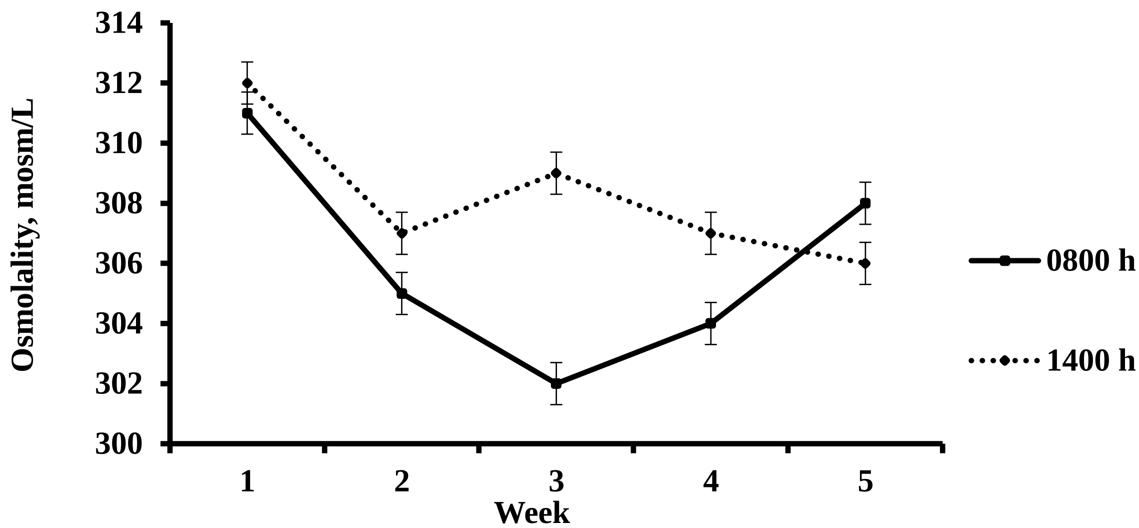


Figure 12. Weekly plasma osmolality differences between times of blood sampling of hair sheep when offered water at 50% of ad libitum intake in period 3.

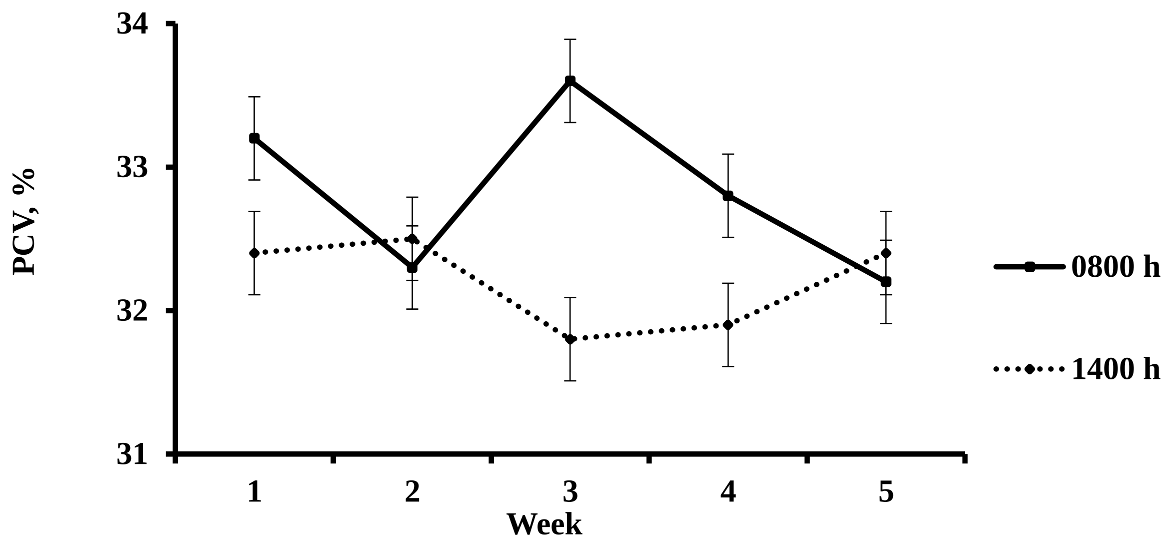


Figure 13. Weekly packed cell volume (PCV) differences between times of blood sampling of hair sheep when offered water at 50% of ad libitum intake in period 3.

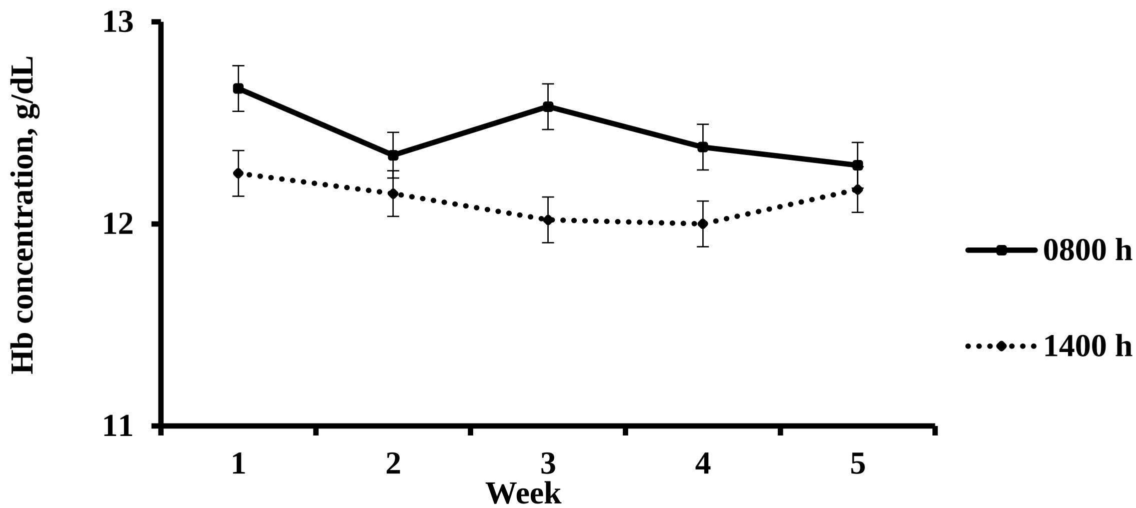


Figure 14. Weekly hemoglobin (Hb) concentration differences between times of blood sampling of hair sheep when offered water at 50% of ad libitum intake in period 3.

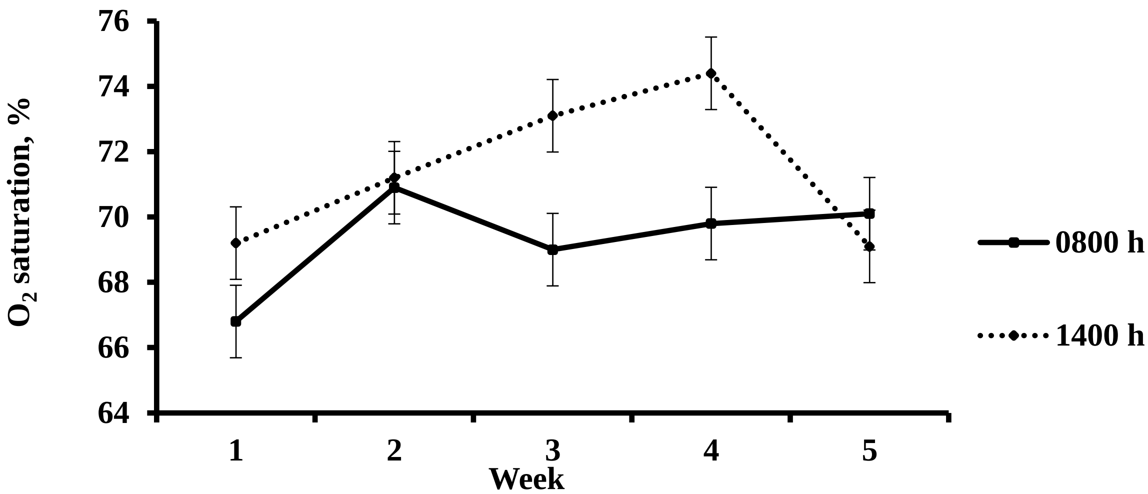


Figure 15. Weekly oxygen saturation differences between times of blood sampling of hair sheep when offered water at 50% of ad libitum intake in period 3.

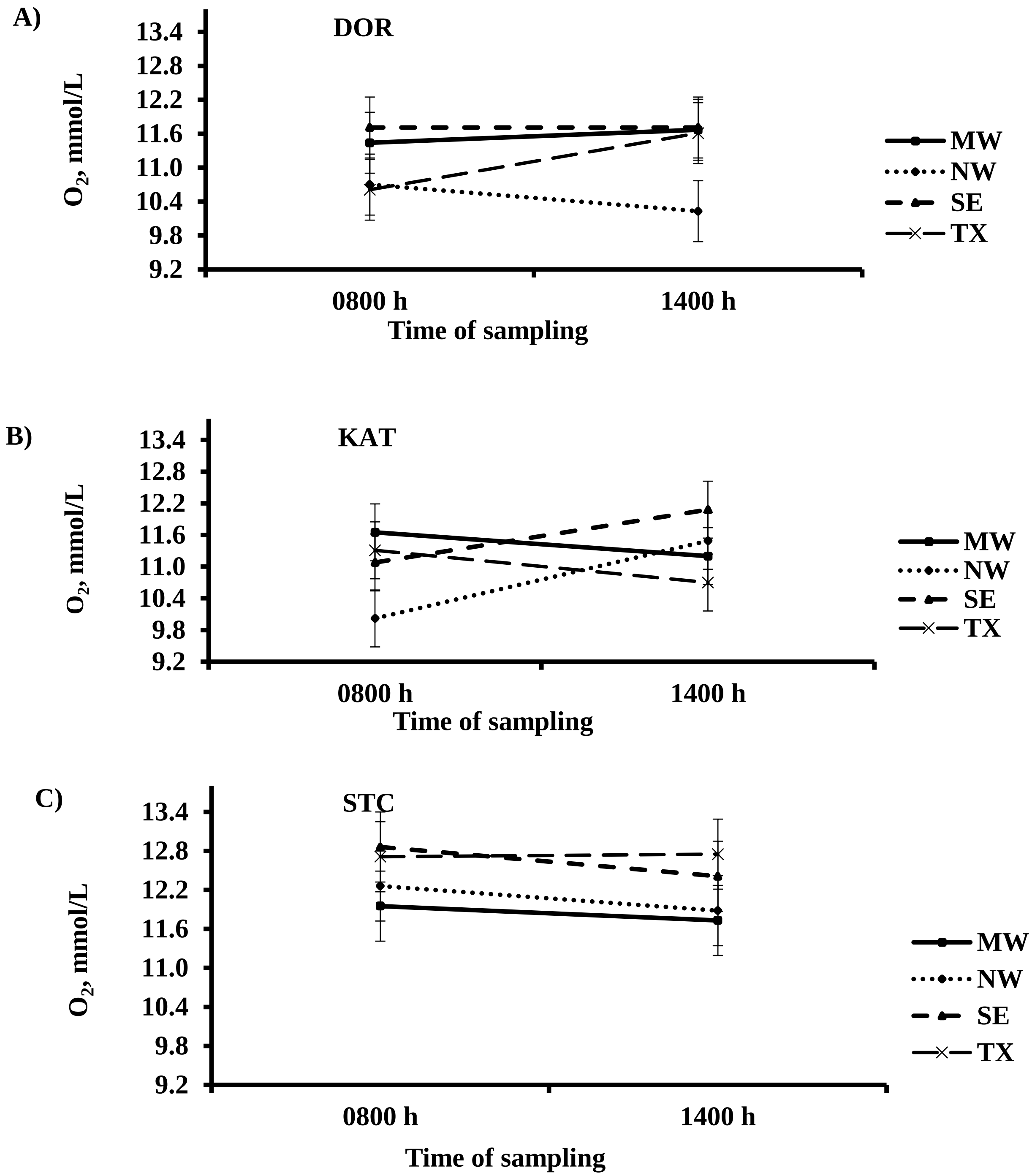


Figure 16. Oxygen (O_2) concentration of Dorper (DOR), Katahdin (KAT), and St. Croix (STC) sheep from the Midwest (MW), Northwest (NW), Southeast (SE), and Central Texas (TX) at different times of blood sampling when offered water at 50% of ad libitum intake during the last 2 weeks of period 3.

CHAPTER V

EFFECTS OF WATER RESTRICTION ON NUTRIENT DIGESTIBILITY AND ENERGY UTILIZATION OF A PELLETED DIET BY ST. CROIX SHEEP

ABSTRACT

Eleven St. Croix ewes (49 ± 8.5 kg initial body weight; BW) were used in a crossover design to evaluate effects of restricted drinking water availability on intake, digestion, and energy utilization of a 50% concentrate pelleted diet containing 19% crude protein (CP) and 34% neutral detergent fiber (NDF) on dry matter (DM) basis. The ewes were housed indoors and fed the diet at 160% of estimated metabolizable energy (ME) requirement for maintenance (71 g DM/kg $BW^{0.75}$). All ewes were offered water ad libitum for 2 wk to determine baseline water intake (WI) by each animal before the study (3,761 ± 144 g/d). The 2-wk baseline was followed by 2 periods of 4 wk each. In each period, 5 or 6 ewes were offered water at 75% of baseline intake for 1 wk and subsequently restricted to 50% (REST) for 3 wk, while the other ewes were offered the baseline amount (CONT) for 4 wk. In wk 4 of each period, all ewes were moved to metabolism crates for total collection of feces and urine and for gas exchange measurements. Some water was refused in wk 4, making the actual WI 2,442 and 1,688 g/d for the CONT and REST ewes, respectively (SEM = 171.7). As a result, the actual water consumed by the REST ewes in wk 4 was 69.1% of WI by the CONT ewes. Intake

of DM was not different ($P = 0.582$) between treatments (860 and 811 g/d for the CONT and REST ewes, respectively). Apparent total tract digestibility of DM (67.2 and 62.1%; SEM = 1.30), organic matter (OM; 68.1 and 63.0%; SEM = 1.30), NDF (44.3 and 34.0%; SEM = 2.46), and gross energy (66.1 and 60.8%; SEM = 1.41) were greater ($P < 0.05$) for the REST than the CONT ewes, and CP digestibility tended ($P = 0.072$) to differ (71.1 and 67.2% for the REST and CONT ewes, respectively; SEM = 1.16). However, intakes of digested DM, OM, CP, and NDF were not different ($P \geq 0.391$) between treatments. Urinary energy loss (0.52 and 0.62 MJ/d; SEM = 0.039) was lower ($P = 0.024$) for the REST than the CONT ewes. However, there were no differences in methane energy loss (0.76 and 0.89 MJ/d; SEM = 0.084; $P = 0.213$), heat energy loss (8.60 and 8.33 MJ/d; SEM = 0.437; $P = 0.580$), metabolizability of the diet (50.7 and 55.2%; SEM = 2.16; $P = 0.261$), or retained energy (-0.54 and -0.44 MJ/d; SEM = 0.768; $P = 0.929$) between the REST and CONT ewes, respectively. In conclusion, restricted drinking water availability did not influence DM intake of the diet but increased its digestibility, presumably by increasing digesta residence time in the gastrointestinal tract.
Key words: digestion, energy utilization, hair sheep, water restriction

INTRODUCTION

Research involving limited water availability to livestock has become increasingly important due to the frequency and intensity of droughts caused by climate change in many parts of the world (Thornton et al., 2009; Nardone et al., 2010; Devendra, 2012), including the U.S. (Hatfield et al., 2008). Ruminants are known to be more resilient to limited water availability than nonruminants because the rumen can serve as a water reservoir (Silanikove, 1994). Despite the fact that water is the most important nutrient, studies on ruminants' ability to cope with its shortage have been limited and focused on performance or physiological responses to water restriction strategies with sheep (Aganga et al., 1989; Hamadeh et al., 2006; Kumar et al., 2016) or goats (Alamer, 2006; Mengistu et al., 2007; Kaliber et al., 2016) in arid or semiarid regions. In many cases, water restriction decreased dry matter intake (DMI) by sheep (Jaber et al., 2004; Casamassima et al., 2016), goats (Alamer, 2009; Ahmed and El Kheir, 2004), or both species (Mengistu et al., 2016). Others, however, reported that DMI was not altered by water restriction in sheep (Casamassima et al., 2008) or goats (Kaliber et al., 2016). Notably, the studies evaluating effects of water restriction on digestibility of dietary nutrients by small ruminants have also been limited in number and contradictory. They showed increased nutrient digestibility with reduced DMI (Silanikove, 1985), increased digestibility without altering DMI (Nejad et al., 2014), and no change in either response variable (Hadjigeorgioua et al., 2000).

In a companion paper (Chapter III of this dissertation), responses in body weight (BW) and DMI to limited drinking water availability were evaluated using three hair sheep breeds, including St. Croix, that were derived from four distinct climatic regions of the U.S. The sheep were fed a 51% concentrate pelleted diet to meet 160% of their metabolizable energy (ME) requirements for maintenance, which could be considered ad libitum feed intake. Any possible changes in digestibility and metabolizability of this diet, however, were not determined primarily because the objective there was to examine resilience to water shortage, which required examination of gradual adaptation of 130 sheep housed individually to a final water restriction level of 50% of ad libitum intake. Thus, the present follow-up study was necessary to determine the effects of this water-restriction treatment on nutrient digestibility and energy utilization of that diet by St. Croix sheep.

MATERIALS AND METHODS

Animals and Diets

All experimental procedures were approved by the Langston University Animal Care Committee. Eleven St. Croix ewes (49 ± 8.5 kg initial BW) were housed in a well-ventilated room individually in 1.05 × 0.55 m elevated pens with a plastic-coated expanded metal floor and each pen was fitted with a plastic barrel for feed and a bucket for water. Fecal and urinary excretions were removed daily to minimize odor and maintain air quality. The ewes were fed a pelleted diet containing 50% concentrate on DM basis (Table 1) at 71 g DM/kg of metabolic BW ($BW^{0.75}$) to meet 160% of their metabolizable energy (ME) requirement for maintenance (NRC, 2007). The diet was offered in 2 equal portions at 0800 and 1500 h daily, the amount of feed offered was recorded, and orts were weighed at 0800 h and used to calculate daily DMI by each animal. Before starting the experiment, all ewes were offered water ad libitum for a 2-wk baseline and the amounts offered and refused were weighed and recorded to calculate average daily water intake (WI) by each ewe.

The experimental design was a crossover with 2 periods of 4 wk each. Ewes were randomly allotted to 2 groups (n = 5 and n = 6) that were assigned to 1 of 2 levels of water availability in period 1, control (CONT) and restricted (REST), and subsequently subjected to the other treatment in period 2. The amount of water offered for the CONT ewes was the average consumed by each animal during the 2-wk baseline. In wk 1 of each period, the REST ewes were offered water at 75% of their baseline WI. This level of water offered was intended to facilitate gradual adaptation to the most severe restriction level of 50%. In wk 2-4 of each period, the REST ewes were offered water at 50% of their baseline WI. The specific amounts of water for each animal in the CONT and REST groups were offered in 2 equal portions each day at 0800 and 1500 h. In wk 4, all ewes were moved to metabolism crates (0.7 × 1.2 m) for total collection of feces and urine. Eight of those crates were located in the same room as the elevated pens and 4 additional crates were situated in a calorimetry room. All ewes were kept in the calorimetry room for 48 h (3 to 4 ewes at a time) to obtain gas exchange measurements. The BW of each ewe was determined on Monday of each week and all ewes were also weighed when they entered and exited the calorimetry room. At the end of each period, the REST ewes were gradually rehydrated to baseline WI by increasing the amount of water offered by 10% of the baseline every 2 d. This gradual increase in water availability after prolonged restriction was implemented to maintain health and prevent hemolysis. Following rehydration in period 1, there was a 1-wk washout period where the ewes were moved outside to a small pasture.

Sample Collection and Measurements

Feed samples were taken daily to form composite samples for each week and stored for later analysis. While the ewes were kept in metabolism crates in wk 4 of each period, their orts were collected daily to form a composite sample for that week. Total feces and urine excreted by each ewe were also collected separately each day over 6 d with the urine being collected in buckets containing 20% (vol/vol) sulfuric acid to maintain pH below 3.0 and prevent volatilization of ammonia. Approximately 10% each of the feces and urine were sampled daily, stored at -20 ^{o}C, and composited for later analysis.

In the calorimetry room, each of the metabolism crates was fitted with a Lexan® (General electric, New York, NY) head box (41 cm width, 27 cm depth, and 92 cm height) to measure consumption of O_2 and production of CO_2 and CH_4 in a an open-circuit respiration calorimetry system (Sable Systems International, Las Vegas, NV). Each head box included a removable drawer (23 cm height in the front, 15 cm height in the back closest to animal, 40 cm width, and 28 cm depth) for feeding and watering with a head opening (30.5 cm wide and 55 cm high beginning at the top of the drawer). A sock of Cordura® nylon (DuPont,Wilimington, DE) attached to the opening of the head box fitted with a 25 cm long zipper was held snug to the neck of each ewe with Velcro® (Velcro USA Inc., Manchester, NH) and Elastikon™ ties (Johnson & Johnson, New Brunswick, NJ) to prevent looseness in the sock and avoid chewing of the material. The operating procedures of the calorimetry system used and sampling of air for analyses were similar to those of Puchala et al. (2007; 2009). Oxygen concentration was analyzed using a fuel cell FC-1B O_2 analyzer (Sable Systems International) whereas CH_4 and CO_2 concentrations were measured with infrared analyzers (CA-1B for CO_2 and MA-1 for CH_4; Sable Systems International). Prior to gas exchange measurements, the analyzers were calibrated with gases of known concentrations and ethanol burn tests were performed to verify complete recovery of O_2 and CO_2 produced under the same flow rates used during the measurements.

Samples of feed and feces were dried in a forced-air oven at 55 ^{o}C for 48 h and ground to pass through a 1-mm screen. The samples were analyzed for DM and ash

(AOAC, 2006), nitrogen (Leco TruMac CN, St. Joseph, MO), gross energy (GE) using a bomb calorimeter (Parr 6300; Parr Instrument Co., Inc., Moline, IL), and neutral detergent fiber (NDF) following the procedures of Van Soest et al. (1991) and using an ANKOM200 Fiber Analyzer (filter bag technique; ANKOM Technology Corp., Fairport, NY). Urine samples were lyophilized (Stellar Freeze Dryer, Millrock Technology, Kingston, NY) to determine DM and conduct other analyses. Nitrogen and GE concentrations in lyophilized urine samples were determined as described earlier and nitrogen percentages were multiplied by 6.25 to estimate crude protein (CP).

Means for daily DMI and WI for wk 4 of each period were calculated using all 7 d of the week and DMI relative to $BW^{0.75}$ was also based on average BW during wk 4 of each period. Heat energy (HE) values in kJ/kg $BW^{0.75}$ were based on the BW immediately recorded before and after taking the calorimetry measurements and were multiplied by average BW in wk 4 of each period to estimate HE in MJ/d. Energy lost as CH_4 was total CH_4 emitted in L/d × 39.5388 kJ/L (Brouwer, 1965), and ME was the difference between digestible energy (DE) and the sum of energy losses in urine and methane. The HE estimates were based on the Brouwer (1965) equation without considering urinary nitrogen. Retained energy (RE) was the difference between ME intake and HE. Heart rate (HR) was monitored as described by Puchala et al. (2009) to determine the ratio of HE to HR. All ewes were fitted with 10 × 10 cm electrodes prepared from stretch conductive fabric (Less EMF, Albany, NY), glued to ECG electrodes (VermedPerformancePlus, Bellows Falls, VT), and attached to the chest slightly below the left elbow and behind the shoulder blade on the right side of the body. Electrodes were connected by ECG snap leads (Bioconnect, San Diego, CA) to T61 coded transmitters (Polar, Lake Success, NY). Human S610 HR (Polar) monitors with wireless connection to the transmitters were used to collect HR data at 1-min intervals and HR data were analyzed using Polar Precision Performance SW software.

Statistical Analyses

Data were analyzed using the MIXED procedure of SAS 9.4 (SAS Institute Inc., Cary, NC). The statistical model included treatment and period as fixed effects, with period as a repeated measure and ewe as the random effect. Means were separated using the LSMEANS statement of SAS. Statistical significance was declared at $P < 0.05$ and tendencies were discussed for $0.05 < P < 0.10$.

RESULTS

Water and Feed Intakes

In wk 1 to 3 of each period, the REST ewes consumed all the water offered. As to WI and DMI during wk 3 (Table 2), the REST ewes consumed 50% of the water consumed by the CONT ewes. They also had an 8.2% lower ($P < 0.05$) DMI in g/d and a tendency for a lower ($P < 0.05$) DMI in g/kg $BW^{0.75}$ than the CONT ewes. When the ewes were moved to the metabolism crates and the calorimetry room in wk 4 of each period, some water was refused by most ewes on both treatments, causing WI by the REST ewes in wk 4 to be higher than 50% of ad libitum intake (Table 3). The reductions in WI by the CONT and REST ewes from wk 3 to wk 4 were 34.6 and 10.3%, respectively. These reductions caused WI by the REST ewes in wk 4 to be 69.1% of WI by the CONT ewes. When WI and DMI by the ewes on both treatments during the days inside the calorimetry room were compared with their intakes in the remaining days of wk 4 outside the calorimetry room (data not shown), WI was 853 g/d lower ($P < 0.05$)

and DMI was 140 g/d lower ($P < 0.05$). However, when DMI in g/d was calculated using all 7 d, there was no difference ($P = 0.582$) between treatments. There were also no differences ($P \geq 0.669$) between treatments for intakes of DM, CP, organic matter (OM), or NDF on a $BW^{0.75}$ basis in wk 4 (Table 3).

Digestibility of Nutrients

Mean digestibilities of each nutrient are shown in Table 3. On a percentage basis, digestibilities of DM, OM, and NDF were greater ($P < 0.05$) for the REST than for the CONT ewes. For example, digestibilies of DM, OM, and NDF were 5.1, 5.1, and 10.3 percentage units higher and 8.2, 8.1, and 30.3% greater for the REST than for the CONT ewes, respectively. Similarly, digestibility of CP tended ($P = 0.072$) to be 3.9 percentage units higher and 5.8% greater for the REST than for the CONT ewes. The quantity of DM, CP, OM, and NDF digested in g/d, however, did not differ ($P \geq 0.391$) between treatments. Retention of nitrogen intake was also similar ($P = 0.729$) between treatments.

Energy Measurements

The *P* values and means for all energy measurements are presented in Table 4. There were no differences ($P \geq 0.584$) in GE intake in MJ/d or in kJ/kg $BW^{0.75}$ between treatments. However, GE digestibility (%) was greater ($P < 0.05$) for the REST than for the CONT ewes by 5.3 percentage units and 8.7%, but DE in MJ/d did not differ ($P = 0.926$) between treatments. Fecal energy loss tended to be greater ($P = 0.089$) for the CONT than for the REST ewes by 0.96 MJ/d. Urinary energy loss was greater ($P < 0.05$) for the CONT than for the REST ewes by 0.10 MJ/d, but urinary energy loss as a percentage of GE and DE did not differ ($P \geq 0.198$) between treatments. Methane energy loss in MJ/d and as a percentage of GE and DE was not different ($P \geq 0.213$) between treatments. Intakes of ME in MJ/d and in kJ/kg $BW^{0.75}$ were similar ($P \geq 0.913$) for the CONT and REST ewes. Expressed as a percentage of GE and DE, ME did not differ ($P \geq 0.261$) between treatments. There were also no differences ($P \geq 0.580$) in HE losses between the CONT and REST ewes in MJ/d, kJ/kg $BW^{0.75}$ or in kJ/kg $BW^{0.75}$ relative to HR. Lastly, RE did not differ ($P \geq 0.849$) between treatments in MJ/d or in kJ/$kg^{0.75}$.

DISCUSSION

Water and Feed Intakes

In wk 3, restriction of WI to 50% of ad libitum decreased DMI by 8.2% from that of the CONT ewes. Many studies with small ruminants revealed more severe reductions in DMI in response to water restriction, including the 50% level tested in the present study. Offering water to Aardi does at 75 and 50% of ad libitum intake for 6 d decreased DMI by 14 and 22%, respectively (Alamer, 2009). Mengistu et al. (2016) reported reductions in DMI of 30.6 and 43.8% by Katahdin sheep, 22.4 and 34.4% by Boer goats, and 19.1 and 35.2% by Spanish goats when their WI decreased gradually by 10% from 100% to 50 and 40% of ad libitum, respectively. Offering water to Lacaune ewes at 80 or 60% of ad libitum intake for 4 wk decreased DMI by 16 and 36% (Casamassima et al., 2016) whereas offering water low or high in total dissolved solids to Baluchi lambs at 50% of ad libitum intake for 6 wk decreased DMI by 40 and 42%, respectively (Vosooghi-Postindozet al., 2018). Offering water to Awassi ewes every 2 or 4 d for 6 wk also decreased DMI by 24 and 44%, respectively (Jaber et al., 2004). Earlier water restriction studies reviewed by Silanikove (1992) also demonstrated this strong relationship between DMI and WI. The severity of DMI reductions in response to water restriction, however, has been shown to be influenced by weather conditions (Maloiy et al., 2008; Alamer, 2009), animal factors (Parrot et al., 1996; Silanikove, 2000) and the diet (van der Walt et al., 1999; Ahmed and El Kheir, 2004). As to the latter, the reduction in DMI caused by dehydration seemed to depend on the type of feed available to the animals. Offering water at 50% of ad libitum intake to Merino sheep on low-protein (oats hay; 5.4% CP) or medium-protein (oats hay plus urea; 10.3% CP) diets decreased DMI by 15 and 29%, respectively (van der Walt et al., 1999). Restricting WI by desert goats to about 40% of ad libitum also decreased DMI of alfalfa (19.7% CP) and grass (5.3% CP) hays by 19 and 21%, respectively (Ahmed and El Kheir, 2004). The variations in dietary ingredients and type of animals used, however, make it difficult to differentiate the effects of water restriction, per se, from those due to the feed consumed.

In the present study, the 8.2% lower DMI by the REST than the CONT ewes in wk 3 was minor in comparison to the severe reductions in DMI reported by others using the same 50% of ad libitum water restriction level with sheep (Vosooghi-Postindozet al., 2018), goats (Alamer, 2009), or both (Mengistu et al., 2016). That 8.2% decrease in DMI, however, resembled a 4.5% reduction in DMI observed when we restricted WI by 44 St. Croix ewes to 50% of ad libitum intake over 5 wk (Chapter III of this dissertation). The minor reductions in DMI in both studies suggest that St. Croix sheep have high ability to adapt and cope with severe shortage in drinking water up to 50% of ad libitum intake. Putting the CONT and REST ewes in the calorimetry room in wk 4 resulted in lower WI and DMI by both treatment groups than their intakes in wk 3. As a result, WI by the REST ewes in wk 4 was 69.1% of WI by the CONT ewes instead of the 50% target level that had been maintained in wk 2 and wk 3 of each period. The reductions in DMI were 312 and 265 g/d lower in wk 4 than in wk 3 for the CONT and REST ewes, respectively.

The reductions in WI and DMI in wk 4 suggest possible stress from constraining the ewes inside (head boxes) and outside (metabolism crates) the calorimertry room and reflected changes in the eating behavior by all ewes regardless of their treatment. Even though DMI was 49 g/d greater for the CONT than the REST ewes in wk 4, the lack of statistical significance could be explained by the large variations in DMI among the ewes as the standard error for DMI rose from 46.0 g/d in wk 3 to 84.8 g/d in wk 4.

The lack of significant change in DMI with water restriction in wk 4, however, was consistent with results of others (Casamassima et al., 2008; Kaliber et al., 2016). When Comisana ewes were offered water ad libitum versus at 80 or 60% of ad libitum intake, DMI did not differ (Casamassima et al., 2008). Similarly, DMI by crossbred German Fawn does was not altered by restricting the water offered to 87 or 73% of ad libitum intake but decreased by 13.1% of ad libitum DMI when the water restriction level was 56% of ad libitum intake (Kaliber et al., 2016). The fact that DMI in the studies by Casamassima et al. (2008) and Kaliber et al. (2016) was not altered by restricting drinking water to 60 or 73% of ad libitum intake, respectively, is consistent with our finding that the 69.1% actual water restriction level in wk 4 was not severe enough to negatively influence DMI. Our findings also suggest that there is a threshold that needs to be reached before a shortage in water availability affects feed intake. In a study examining the relationship between water restriction and feed intake, Hadjigeorgiou et al. (2000) concluded that adequate levels of drinking water such as 70.8 and 73.5% of ad libitum intake was essential for proper digestive function without affecting DMI by Karagouniko sheep.

Digestibility of Nutrients

The greater digestibilities of DM, OM, NDF, and CP by the REST relative to the CONT ewes were likely caused by a slower rate of digesta passage and longer retention time of digesta in the gastrointestinal tract which, in turn, would have improved digestibility of nutrients (Van Soest, 1982). Considering that DMI by the CONT and REST ewes did not differ in wk 4, it is possible that the slower passage rate was directly influenced by the quantity of water consumed (Kaske and Groth, 1997). Passage rate of fluid through the gastrointestinal tract is known to decrease as an adaptation mechanism by ruminants during water restriction in order to use the rumen as a water reservoir and retain more water in the body (Silanikove, 1994). Decades earlier, Balch et al. (1953) demonstrated that water restriction tended to decrease rate of digesta passage in cattle. Later studies reported improvements in digestibility of DM, CP, and other nutrients in water-restricted cattle (Thornton and Yates, 1968) and sheep (Asplund and Pfander, 1972) and suggested the improvement to have been caused by a slower rate of digesta passage.

Other studies also reported improved digestibility of nutrients in water-restricted sheep and goats. Silanikove (1985) reported that restricting water availability to desert and non-desert goats from ad libitum each day to every 3 d decreased DMI by 11.9 and 39.7 g/kg $BW^{0.75}$ and increased DM digestibility of alfalfa hay from 71.6 to 74.1 and from 66.8 to 71.2, respectively. Vosooghi-Postindoz et al. (2018) also reported that water restriction to 50% of ad libitum intake decreased DMI and improved digestibilies of OM, NDF, acid detergent fiber (ADF), and CP by Baluchi lambs having free access to a diet containing 40% alfalfa hay. In contrast, Freudenberger and Hume (1993) showed that digestibilities of DM and ADF did not improve when mature goats having free access to alfalfa hay were restricted to 57% of ad libitum WI. Hadjigeorgioua et al. (2000) also did not detect any improvement in disgestibilities of DM, NDF, ADF, or CP when Karagouniko sheep had free access to an alfalfa hay diet but offered water ad libitum throughout the day, for 1 h daily, or at 65% of ad libitum intake. Considering that the goats and sheep in those two studies were fed chopped alfalfa hay that varied in CP contents (8.1 versus 12.8%, respectively), it is possible that other factors contributed to the lack of improvement in digestibilities.

In agreement with our results in wk 4, Nejad et al. (2014) found that restricting water offered to Corriedale ewes from ad libitum throughout the day to 2 h after feeding did not alter DMI but improved digestibilities of NDF and CP of a maintenance diet similar to ours in forage to concentrate ratio by 6.6 and 3.9 percentage units, respectively, and increased retained nitrogen from 20.0 to 31.1% of nitrogen intake. In the present study, digestibilities of NDF and CP were improved by 10.3 and 3.9 percentage units, respectively, and retained nitrogen numerically increased from 11.5 to 16.3% of nitrogen intake. In both studies, increased nitrogen retention was a result of improved digestibility of CP and decreased nitrogen excretion in the urine. The latter suggests improved efficiency of nitrogen recycling through the rumen wall and saliva for microbial protein synthesis under the water restrictions used in both studies.

Although high variability in DMI during wk 4 of our study contributed to the lack of significant difference in DMI, the numerical differences in wk 4 DMI cannot be excluded as a possible explanation for treatment differences in digestibility of DM, OM, NDF, and CP. The fact that the quantity of digested DM, OM, NDF, and CP did not differ between treatments supports the idea that increases in digestibility as a percentage with water restriction was related to a numerical decrease in DMI. When the same pelleted diet was evaluated in our laboratory (Tadesse et al., 2019), greater digestibilities of DM, OM, NDF, and CP were found when mature Katahdin wethers were feed restricted at 55% of their ME requirements for maintenance than wethers fed near their maintenance energy requirements. Those increases in digestibility with feed restriction were assumed to have resulted from longer residence time of digesta in the rumen (Tadesse et al., 2019).

Energy Measurements

The lack of differences in GE intake between the CONT and REST ewes in wk 4 was a result of the similar DMI by both groups. The greater digestion of GE by the REST ewes was consistent with the increases in DM, OM, and NDF digestibilities and could be related to changes in ruminal retention time or passage rate through the gastrointestinal tract. When the same pelleted diet was offered to Katahdin wethers (Tadesse et al., 2019), increases in GE digestibility occurred in wethers consuming less GE and decreases in ME intake occurred in wethers consuming less feed. The lower ME intake in feed-restricted wethers were due to fecal energy, urinary energy, and methane energy losses being either lower or tending to be lower in wethers offered less feed. In the present study, the REST ewes had lower urinary energy loss than the CONT ewes without differences in methane energy losses or ME intake. However, the lack of difference in ME intake was partially due to the large variability as daily ME intake was 0.10 MJ lower in the REST ewes.

Studies that measured energy losses or changes in energy retention in small ruminants during water restriction are limited. Steiger Burgos et al. (2001) investigated possible digestive or metabolic mechanisms activated by dairy cows during water restriction to 50% of ad libitum intake. They found that the cows compensated for decreased DMI by decreasing milk production, increasing digestibility of OM, and improving efficiency of energy utilization by decreasing heat production, methane production, and energy needs for maintenance. Although the water restriction level used with the cows was identical to the 50% of ad libitum intake target used in our ewes, there were clear differences in the results. In contrast to the lower DMI, HE loss, and methane energy loss in cows consuming water ad libitum versus at 50% of ad libitum intake, there were no differences in those measurements between our CONT and REST ewes. The contradictory results for DMI, HE loss, and methane energy loss between the two studies, however, could be explained by the fact that actual water restriction during wk 4 was 69.1% of WI by the CONT ewes instead of the 50% target level that had been maintained in wk 2 and wk 3 of each period. Therefore, it appears that the 69.1% restriction level was not severe enough to produce results similar to those of Steiger Burgos et al. (2001).

It is worth noting that in the study by Steiger Burgos et al. (2001), the effect of water restriction on HE loss was confounded by changes in DMI. The confounding effects of reduced DMI and WI made it difficult to determine if limited WI can directly and independently cause changes in heat production. A study by Li et al. (2000) was the first to separate the confounding effects of DMI and WI on heat production by having adult sheep fasted for 3 d and not offering water to half of the fasted animals. Although fasting decreased heat production, Li et al. (2000) did not report further reductions as a result of water restriction. Lack of change in heat production with water restriction alone was consistent with our ewes and with Chokla sheep in the study by More (1984) in which no changes in metabolic activity or heat production were reported when water was offered once every 3 d. The similar HE loss for the treatment groups in the present study would also explain the similar RE values in the CONT and REST ewes.

CONCLUSION

Restricted drinking water availability increased digestibility of a 50% concentrate pelleted diet, possibly by increasing residence time of digesta in the gastrointestinal tract. Utilization of ME was not different between ewes consuming water ad libitum or at 69.1% of ad libitum intake and the lack of difference in energy utilization was most likely a function of smaller differences in DMI between treatments when St. Croix ewes were undergoing calorimetry measurements.

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Table 1. Ingredient and nutrient composition of diet fed to St. Croix ewes

Item	Concentration
Ingredient, % as fed basis	
Cottonseed hulls	29.06
Ground corn	19.98
Dehydrated alfalfa	19.98
Wheat middlings	13.00
Cottonseed meal	8.99
Pelleting agent	4.99
Salt	1.00
Calcium carbonate	0.95
Ammonium chloride	1.00
Yeast	1.00
Vitamin-mineral mix[1]	0.05
Rumensin 90 premix[2]	0.01
Nutrient composition, dry matter basis[3]	
Ash, %	8.9 ± 0.07
Crude protein, %	19.4 ± 0.13
Neutral detergent fiber, %	33.6 ± 0.26
Gross energy, MJ/kg	17.0 ± 0.01

[1]Composition: 1.28% Zn; 0.96% Fe; 0.704% Mn; 0.16% Cu; 0.048% I; 0.032% Co; 26,460,000 IU/kg vitamin A; 6,615,000 IU/kg vitamin D_3, and 11,025 IU/kg vitamin E.
[2]Supplied 20% monensin.
[3]Analysis of weekly composite samples formed from daily samples.

Table 2. Effects of level of water offered on intake of water and dry matter by St. Croix ewes during wk 3 of each period

	Treatment[1]			
Item[2]	CONT	REST	SEM	*P* value
Water intake, g/d	3,733	1,881	173.5	<0.001
Dry matter intake				
g/d	1,172	1,076	46.0	0.036
g/kg $BW^{0.75}$	61.6	57.8	1.47	0.089

[1]Control (CONT) ewes were offered water at ad libitum (baseline) intake whereas restricted (REST) ewes were offered water at 50% of baseline intake.
[2]BW = body weight.

Table 3. Effects of level of water offered on intake and digestion of dry matter, organic matter, crude protein, and neutral detergent fiber, water intake, and retention of consumed nitrogen by St. Croix ewes during wk 4 of each period

	Treatment[1]			
Item[2]	CONT	REST	SEM	*P* value
Water intake, g/d	2,442	1,688	171.7	0.002
Dry matter				
Intake, g/d	860	811	84.8	0.582
Intake, g/kg $BW^{0.75}$	45.9	44.0	4.12	0.672
Digested, g/d	540	543	59.0	0.959
Digestion, %	62.1	67.2	1.35	0.028
Organic matter				
Intake, g/kg $BW^{0.75}$	42.0	40.2	3.76	0.672
Digested, g/d	500	503	54.2	0.965
Digestion, %	63.0	68.1	1.34	0.027
Neutral detergent fiber				
Intake, g/kg $BW^{0.75}$	15.7	15.0	1.43	0.669
Digested, g/d	103	119	14.5	0.391
Digestion, %	34.0	44.3	2.41	0.013
Nitrogen				
Intake, g/d	26.0	24.5	2.55	0.584
Intake, g/kg $BW^{0.75}$	1.4	1.3	0.12	0.673
Digested, g/d	17.7	17.5	1.93	0.920
Digestion, %	67.2	71.1	1.32	0.072
Urinary excretion, g/d	14.6	12.6	0.73	0.064
Balance, g/d	3.0	4.0	1.82	0.729
Crude protein				
Intake, g/kg $BW^{0.75}$	8.7	8.3	0.78	0.672
Digested, g/d	111	109	12.1	0.920
Digestion, %	67.2	71.1	1.32	0.072

[1]Control (CONT) ewes were offered water at ad libitum (baseline) intake whereas restricted (REST) ewes were offered water at 50% of baseline intake.
[2]BW = body weight.

Table 4. Effects of level of water offered on energy measurements in St. Croix ewes during wk 4 of each period

	Treatment[1]			
Item[2]	CONT	REST	SEM	*P* value
Gross energy				
Intake, MJ/d	15.35	14.49	1.509	0.584
Intake, kJ/kg $BW^{0.75}$	814	779	72.6	0.673
Digested, MJ/d	9.45	9.55	1.04	0.926
Digestion, %	60.8	66.1	1.41	0.026
Urinary energy losses				
MJ/d	0.62	0.52	0.039	0.024
% gross energy	4.65	3.84	0.539	0.297
% digestible energy	7.75	5.89	0.920	0.198
Fecal energy losses				
MJ/d	5.90	4.94	0.542	0.089
Methane energy losses				
MJ/d	0.76	0.89	0.084	0.213
% gross energy	5.4	6.3	0.52	0.333
% digestible energy	9.0	9.6	0.95	0.716
Metabolizable energy				
Intake, MJ/d	8.06	7.96	1.023	0.939
Intake, kJ/kg $BW^{0.75}$	426	433	50.7	0.913
% gross energy (metabolizability)	50.7	55.2	2.16	0.261
% digestible energy	83.3	84.2	1.75	0.747
Heat energy				
MJ/d	8.60	8.33	0.437	0.580
kJ/kg $BW^{0.75}$	459	448	17.4	0.649
kJ/kg $BW^{0.75}$/(heart beats/min)	6.41	6.35	0.138	0.767
Retained energy				
MJ/d	-0.54	-0.44	0.768	0.929
kJ/ kg $BW^{0.75}$	-33.8	-22.1	41.81	0.849

[1]Control (CONT) ewes were offered water at ad libitum (baseline) intake whereas restricted (REST) ewes were offered water at 50% of baseline intake.
[2]BW = body weight.

CHAPTER VI

SUMMARY AND CONCLUSIONS

The rising temperatures and expansion of droughts due to climate change represent major threats to animal agriculture worldwide and require conditioning ruminants to survive, thrive, and possibly produce at levels matching their genetic potential under harsh environmental conditions. This could be achieved by selection and development of resilient animals. Hair sheep breeds have been spreading worldwide because of their higher fertility, prolificacy, survivability, resistance to gastrointestinal parasites, and production of meat than wool sheep raised under similar conditions. As a consequence of their economical viability, Dorper, Katahdin, and St. Croix have become major hair sheep breeds in the U.S. However, despite their importance to the U.S. sheep industry and their adaptability to adverse climates, they have not been evaluated for resilience to limited drinking water availability. Thus, the objective of the research presented in this dissertation was to establish a performance, physiological, and nutritional assessment of hair sheep tolerance to severe water shortage.

In Experiment 1, the resilience of the 3 hair sheep breeds, which represented 4 climatic U.S. regions (i.e., the Midwest, Northwest, Southwest, and central Texas), to water restriction was evaluated in 4 separate 9-wk trials over 2 yr. In each trial, all breeds and regions were represented and all sheep were housed individually under temperature and humidity within their comfort threshold, were fed a pelleted diet at 160% of the metabolizable energy requirement for maintenance, and were offered water at 50% of ad libitum intake for 5 wk following a baseline and intermediate water restriction periods of 2 wk each in which the sheep were offered 100 and 75% of ad libitum water intake, respectively. Performance and physiological responses of 130 ewes were assessed each week and the data from the 4 trials were pooled and analyzed for main effects of and interactions involving breed, region, period, week within period, and time of blood sampling within a week using different statistical models for different response variables. Across breeds and regions, the sheep decreased dry matter intake with advancing water restriction, gained weight when switched to 75% water restriction, suffered minor weight losses in wk 1 of 50% restriction, and gained weight in the remaining 4 wk of that restriction. Assessment of blood measurements and metabolites sensitive to water shortage revealed that across breeds and regions, all sheep exhibited minor changes in packed cell volume, hemoglobin concentration, plasma osmolality, and serum concentrations of albumin, cholesterol, creatinine, glucose, lactate, total protein, triglycerides, and urea under 75% water restriction. All sheep needed 1 wk to adapt to the severe water shortage of 50% and maintained levels of blood measurements and metabolites that were slightly higher than baseline values thereafter.

In Experiment 2, nutrient digestibility and energy utilization of the diet fed in Experiment 1 were determined in a crossover design in which 11 St. Croix ewes were offered water at 50 or 100% of ad libitum intake. Water restriction increased apparent digestibility of dry matter, organic matter, neutral determent fiber, and crude protein, but did not affect energy utilization. It was concluded that the 3 hair sheep breeds had high resilience to limited water availability in the absence of heat stress and that improved digestibility of dietary nutrients was an adaptation mechanism that enabled them to gain weight under the severe water shortage.

VITA

Ali Hussein Hussein

Candidate for the Degree of

Doctor of Philosophy

Dissertation: RESILIENCE OF SHEEP TO LIMITED WATER AVAILABILITY

Major Field: Animal Science

Biographical:

Education:

Completed the requirements for the Doctor of Philosophy in Animal Science at Oklahoma State University, Stillwater, Oklahoma in May, 2019.
Completed the requirements for the Master of Science in Animal Science at Kansas State University, Manhattan, Kansas in August, 2015.
Completed the requirements for the Bachelor of Science in Animal Science at the University of Minnesota, St. Paul, Minnesota in May, 2013.

Experience:

Research Assistant, E Kika de la Garza American Institute for Goat Research, Langston University, Langston, Oklahoma, 2015-2019; Graduate Teaching Assistant, Department of Animal and Food Sciences, Oklahoma State University, Stillwater, Oklahoma, 2015-2017; Graduate Research and Teaching Assistant, Department of Animal Sciences and Industry, Kansas State University, Manhattan, Kansas, 2013-2015; Undergraduate Intern, United States Department of Agriculture-Agricultural Research Service, St. Paul, Minnesota, 2011.

Professional Memberships:

Phi Kappa Phi Honor Society, American Society of Animal Science, American Dairy Science Association, American Association for the Advancement of Science